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BRITISH PTERIDOLOGICAL SOCIETY

THE FERN GAZETTE

Proceedings of the International Pteridophyte Symposium

Ferns for the 21st Century

Royal Botanic Garden Edinburgh, Scotland, UK
12-16 July 2004

Part 1

EDITORS:

M. GIBBY, A. LEONARD & H. SCHNEIDER

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PROGRAMME
(in chronological order)

P.R. Crane: Palaeobotany and the Diversification of Pteridophytes

K.M. Pryer, E. Schuettpelz, P.G. Wolf, H. Schneider, A.R. Smith & R. Cranfill: Phylogeny and evolution of monilophytes: a new perspective on ferns, with a focus on early-diverging leptosporangiate lineages

R. Cranfill & H. Schneider: Phylogeny of the Pteridoid Ferns

T.A. Ranker, A.R. Smith, B.S. Parris, J.M.O. Geiger, C.H. Haufler, S.C.K. Straub & H. Schneider: Phylogeny and evolution of grammitid ferns (Grammitidaceae): a case of rampant morphological homoplasy

C. Tsutumi & M. Kato: Phylogeny and evolution of epiphytes and related ferns

J. Pahnke: Molecular evolution of rDNA internal transcribed spacer sequences from the inverted repeats of chloroplast genomes in Pteridophytes

R. Kirkpatrick: A phylogenetic hypothesis and monophyletic circumscription of *Pellaea*

L. Huiet & A.R. Smith: Phylogenetic relationships in *Adiantum* inferred from chloroplast coding and non-coding sequences

W.C. Taylor & S.B. Hoot: Phylogeny of *Isoëtes* based on nucleotide sequences of the nuclear ribosomal ITS region and the second intron of a *LFY* homolog

M.J.M. Christenhusz & H. Tuomisto: Taxonomy, biogeography and ecology of *Danaea* (Marattiaceae)

E. Schuettpelz & K.M. Pryer: Rates and dates: insight into the evolutionary history of filmy ferns (Hymenophyllaceae)

A. Ebihara, J.-Y. Dubuisson, K. Iwatsuki & M. Ito: New insights on *Trichomanes* systematics

S. Hennequin, A. Ebihara, M. Ito, K. Iwatsuki & J.-Y. Dubuisson: Phylogenetic systematics and evolution of the genus *Hymenophyllum* (Hymenophyllaceae)

A.R. Smith: Floristics in the 21st Century: Balancing User-Needs and Phylogenetic Information

H. Tuomisto: Ecological distribution of Amazonian pteridophytes

M. Jones: Landscape-scale distribution of tree ferns in relation to environmental variation at the La Selva Biological Station, Costa Rica

M. Kessler: Distribution and evolution of fern endemism in the Bolivian Andes

B.S. Parris: The Grammitidaceae of Mount Jaya, New Guinea, and other montane Malesian localities

M. Lehnert: New insights on Neotropical Cyatheaceae

K. Mehltreter, K. Hülber & P. Hietz: Herbivory on epiphytic ferns of a Mexican cloud forest

J.F. Barcelona: Noteworthy fern discoveries, collections, and observations from the montane forests of Luzon to the lowland karst forests of Bohol, Philippines

J.M. Sharpe: Temporal variation in plant and leaf characteristics of reproductively mature sporophytes of *Dryopteris intermedia* and *Polystichum acrostichoides*, two common understory ferns of the New England forest

K. Rünk, M. Moora & M. Zobel: Do different competitive abilities of three fern species explain their different regional abundances?

S. Blackmore & K. Walter: Cockroaches, rats and horsetails

D. Ballesteros, E. Estrelles & A.M. Ibars: Pteridophytic spore responses to ultra freezing temperatures for long term conservation in germplasm banks

Wen-Liang Chiou, Yao-Moan Huang & G.M. Chen: Conservation of endangered ferns, *Archangiopteris somai* and *A. itoi* (Marattiaceae), by propagation from their stipules

M. Palacios-Rios & G. Ramírez Maldonado: Propagation in vitro of *Sphaeropteris horrida* (Liebm.) Tryon (Pteridophyta: Cyatheaceae), as an alternative method for conservation

L.G. Quintanilla, E. Pangua, J. Amigo & S. Pajaron: Sexual phenotypes of the northernmost populations of *Culcita macrocarpa* (Dicksoniaceae: Pteridophyta) and *Woodwardia radicans* (Blechnaceae: Pteridophyta)

H. McHaffie: Conservation challenges of *Woodsia ilvensis* – attempting to establish reproducing populations

F.J. Rumsey: Reproductive strategies and population structure in the endangered pteridophyte *Trichomanes speciosum* Willd.

G. Rothwell: Fossils, ferns, and patterns of phylogeny

N.S. Nagalingum, H. Schneider, K.M. Pryer, R. Lupia & M. Nowak: Combining evidence from fossils and extant taxa to reconstruct the evolution of heterospory in ferns

R.A. Stockey: Anatomically preserved pteridophytes: unexpected diversity for the early Cretaceous

K.B. Pigg, M.L. DeVore & W.C. Wehr: Tertiary ferns from western North America: *Osmunda*, *Woodwardia* and onocleoids

C.M. Berry, Wang Yi & Li Chengsen: The impact of Chinese Devonian fossils on the search for fern origins

P. Kenrick & J. Hilton: *Polypetalophyton* and the Devonian origin of ferns

E. Iskandar, I. van Waveren, J. van Konijnenburg & R. Wagner: Review of the Permian pecopterids from Sumatra: what can be achieved quantitatively?

C.N. Page: The ecology of long-term evolutionary survival – what can be learned from Pteridophyta

M. Gibby & J.C. Vogel: Speciation and hybridization – reviewing Manton's legacy

J.C. Vogel, S.J. Russell, M. Grundmann, F.J. Rumsey, H. Hunt, H. Schneider, M. Gibby, I. Pintér, S. Trewick, M. Morgan-Richards & J.A. Barrett: Locating long-term glacial refugia in the Mediterranean Basin. Autopolyploid complexes in *Asplenium* as a model system

L. Perrie & P. Brownsey: New Zealand *Asplenium* revisited – DNA Sequencing and AFLP Fingerprinting

V. Krízsik, I. Pintér, Á. Major & G. Vida: Scale analyses of intrapopulation spatial genetic structure of *Asplenium ceterach* L. (Aspleniaceae: Pteridophyta) on the Hungarian Szent György Hills

J. Squirrell, P.M. Hollingsworth, M. Woodhead, J. Russell, M. Gibby & W. Powell: Population genetic structure in *Athyrium distentifolium*

H.V. Hunt, M.E.N. Majerus & J.C. Vogel: Breaking free of one's parents: the problem of polyploid establishment

B.S.C. Leadbeater: Irene Manton (1904-1988) - Legend and Legacy

I.J. Leitch: The ups and downs of genome size evolution in pteridophytes

M. Hasebe: The origin and evolution of diploid body plans – synthesis of evolution and development

T. Janssen & H. Schneider: Dating the evolution of drynarioid humus collectors

E. Sheffield & K. Makgomol: Development of gametophytes from gemmae of Killarney Fern (*Trichomanes speciosum* Willd.)

L. Chinnery: Pteridophytes and their mycorrhizas – an evolutionary perspective

W. Friedman & J. Winther: Endomycorrhizal symbioses in ferns
H.K. Goswami & A.K. Bajpai: Differential molecular phenomena inside the micro and megasporangia of *Isoetes pantii*

POSTERS

S. Aguiar, J. Amigo & L.G. Quintanilla: Does *Blechnum collalense* hybridize with *B. mochaenum* (Blechnaceae: Pteridophyta)?
T. Barbará, & G.J. Gastony: Molecular phylogenetics and systematics of *Pellaea* section *Ormopteris* (Pteridaceae subfamily Cheilanthoideae)
T. Boonkerd: Morphometric relationships between *Colysis* C.Presl and *Leptochilus* Kaulf. (Polypodiaceae: Pteridophyta)
E. Estrelles, J.J. Herrero-Borgoñon & A. M. Ibars: What about *Equisetum hyemale* L. (Equisetaceae: Pteridophyta) in the eastern Iberian peninsula?
M. Hashino, N. Takahashi & R. Imaichi: Comparative development of gametophytes of Polypodiaceae
S. Helfer: Micro-fungal fern pathogens
P. Hovenkamp: *Nephrolepis* - not "the devil's genus"
T. Janssen & M. Lehnert: How to deal with bulky ferns ? – Towards a standardized method for tree fern collections
Y. Krippel: The Pteridophyte diversity in Luxembourg
L.G. Quintanilla, S. Pajarón, E. Pangua & J. Amigo: Allozyme variation in *Culcita macrocarpa* (Dicksoniaceae) and *Woodwardia radicans* (Blechnaceae) at their northern limit
L.G. Quintanilla & A. Escudero: Effect of temperature on germination in seven *Dryopteris* species (Dryopteridaceae) from northern Spain
J.P. Ramos Giacosa, E.R. de la Sota, & G.E. Giudice: Biodiversity and Chorology of Pteridophytes from Buenos Aires Province, Argentina
M. Romanova & J. Jernstedt: Morphogenetic events in the *Ceratopteris Richardii* shoot apex
G. Rouhan, F. Rakotondrainibe, R.C. Moran, J.T. Mickel, T.J Motley & J.-Y. Dubuisson: Molecular phylogeny of the fern genus *Elaphoglossum* (Elaphoglossaceae) based on chloroplast non-coding DNA sequences: contributions of species from the Indian Ocean area
A. Sathapattayanon & T. Boonkerd: Pteridophyte diversity along a gradient of disturbance within and near abandoned opencast mines in Thong Pha Phum District, Kanchanaburi Province, Thailand
J.L. Schmitt & P.G. Windisch: Phenological aspects of frond production in Alsophila setosa Kaulf. (Cyatheaceae: Pteridophyta) in southern Brazil
E. Sheffield & S.E. Siman: Growth Impairment of Human Cells by Fern Spore Extracts
E.R. de la Sota & O.G. Martínez: The pteridophytic diversity in the cloud montane forests from Salta (NW Argentina)
M. Warwick: Fern etchings
J.C. Yesilyurt, M. Gibby & A. Culham: Phylogenetic studies in *Doryopteris* J. Sm. (Pteridaceae- Cheilanthoideae)
E.K. Zenkteler & H. Kwaÿna: Fungistatic activity of internal secreting hairs of *Dryopteris* rhizomes

Proceedings of the meeting will be published in this and following parts of the Fern Gazette, Volume 17.

FLORISTICS IN THE 21ST CENTURY: BALANCING USER-NEEDS AND PHYLOGENETIC INFORMATION

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Key words: pteridophytes, floristics, phylogenetics

ABSTRACT

The status of floristic work on pteridophytes around the world is reviewed. Relatively modern floras exist for most temperate and Mediterranean areas, including Europe, the former Soviet Union, North America north of Mexico, Chile, South Africa, and Australia, but are absent, partial, or outdated for many, if not most, tropical and subtropical countries/regions. Exceptions in the New World include Mexico, Mesoamerica, and certain of the Antilles. For many areas we have only annotated checklists (e.g., Tropical East Africa, Malaysia, Mount Kinabalu) or partially written floras (Ecuador, Malesia). Modern treatments for island floras are also few, exceptions being for New Zealand (Brownsey & Smith-Dodsworth, 2001), Hawaii (Palmer, 2003), and the Mariana Islands (Raulerson & Rinehart, 1992). Floristic "hotspots", e.g., Colombia, Brazil, Madagascar, New Guinea, and the Himalayas, often have inadequate or incomplete modern accounts. Treatments of the ferns are planned or in progress for many countries, including Venezuela, Bolivia, East Africa, and China, but these often proceed at a painstakingly slow pace. Local florulas, such as for Barro Colorado Island in Panama, complement larger regional floras while serving different, but overlapping, purposes; Flora Guaramacal (Venezuela), Central French Guiana (Saül), and the Hong Kong flora are notable examples. Ideally, modern pteridofloras should incorporate recent phylogenetic conclusions at various ranks (especially family, genus), multi-access keys, comments on relationships and taxonomic problems, and references to phylogenetic literature, coupled with access to online data-bases (interactive keys, gazetteers, publication data, distribution maps, images and photographs, specimen citations, trees of relationship, and links to pertinent websites). Two families usually considered "fern allies", Psilotaceae and Equisetaceae, are now thought to be intimately related to basal ferns, and this evidence needs inclusion into floristic literature. Many traditional genera (e.g., *Asplenium*, *Pellaea*, *Polypodium*, *Pteris*) need substantial recircumscription to meet criteria of monophyly or even paraphyly in floras. The dwindling number of people with broad expertise in floristics, fern systematics, and identification seriously constrains the creation of modern floras, and is expected to be an increasing problem in the future.

INTRODUCTION

An overview of the status of floristic work dealing with pteridophytes, particularly those in Malesia, was given almost ten years ago as part of the Holttum Memorial Pteridophyte Symposium, held at Kew in 1995 (Roos, 1996). I re-examine the progress

of floristic research, especially in tropical and subtropical regions, in light of recent floristic accounts and the availability of a multitude of resources and data-bases, many web-based. I also discuss what a modern flora should contain, considering the proliferation of phylogenetic studies. Last, I allude to several practical problems associated with the writing of floras. The subject of floristics is an especially important topic because the writing of a flora offers systematic botanists one of the best opportunities for communicating knowledge of plants to a more general audience and to the public.

PURPOSES OF A FLORA

Forty years ago, Lincoln Constance called systematics "the unending synthesis" (Constance, 1964), and floras are perhaps the quintessential manifestation of this synthetic process. It is generally agreed that the primary goal of a flora is to facilitate the identification of plants in a given area (Diggs & Lipscomb, 2002; Heywood, 2001). There are also several secondary goals of floras (see, e.g., Barkley, 2000; Diggs & Lipscomb, 2002; Sanders & Judd, 2000). These include the following: 1) a means of entrance into the systematic literature; 2) a summary of our current knowledge of various aspects related to the biology of plants, e.g., systematic, distributional, ecological, conservation, biotic interactions, ethnobotanical, cytological, reproductive, physiological, and phylogenetic information; 3) providing a reference for other professionals; 4) stabilizing concepts of taxa, especially families and genera, in the minds of users, a kind of asymptotic process; 5) linking the work of monographers and phylogeneticists to consumers of botanical information; and 6) providing systems of classification and nomenclature that allow comparisons with other floristic works, for example, comparisons of numbers of species, endemics, and introduced taxa from one flora to another.

Given these aims, it becomes obvious that any flora is a series of compromises, i.e., providing enough information to make likely the greatest utility for most users. The floristic plan must be executed given constraints of knowledge, access to specimens and library resources, space, time, money, publisher-imposed requirements, and technical support. The writing of a flora involves the translation and synthesis of many different kinds of information about plants into a form that can be used by individuals with varying interests, training, and backgrounds. An important goal for anyone conducting floristic research should be critical re-evaluation of existing circumscriptions, especially at species rank. To be avoided is a process Heywood (2001) has called "superficial compilation", which characterizes some floras.

The region of coverage of a flora may be very broad, such as the Flora of North America north of Mexico, (including Greenland), ca. 21.5 million km^2 (Flora of North America Editorial Committee, 1993a); or quite narrow, e.g., Barro Colorado Island (Panama), 15.6 km^2 (Croat, 1978). It may be dictated by political boundaries (e.g., The pteridophytes of Mexico; Mickel & Smith, 2004); or phytogeographic in scope (Flora of the Venezuelan Guayana; Smith, 1995). The users of a flora include professional systematists and other scientists, students, interested amateurs, governmental workers, those charged with writing environmental impact reports, and others (Diggs & Lipscomb, 2002).

Floras, florulas, and related products run the gamut from bare checklists (e.g., Salgado, 1990, for Philippine ferns; Parris & Latiff, 1997, for Malaysian pteridophytes), to annotated lists lacking descriptions but giving brief synonymy, habit, references,

ranges, and voucher information, e.g., the Ecuador flora (Jørgensen & León-Yánez, 1999) or the treatment of the ferns of Mt. Kinabalu (Parris et al., 1992), to more traditional statements with keys, accepted names, minimal synonymy, diagnoses or brief descriptions, and a statement of range, e.g., Flora Europaea (Tutin et al., 1993). Sometimes, floras are much more elaborate, e.g., Øllgaard & Tind's (1993) work on Scandinavian ferns, which includes also information on ecology, reproduction, spore morphology, etymology, morphological variation, relationships, and ethnobotanical uses, as well as elaborate colour paintings and line illustrations, for each species. Temperate areas, in general, have better coverage (and fewer pteridophyte species) than do floras in the tropics. No single plan suits every purpose, or is appropriate given the information base available. In fact, our ideas about what constitutes a proper flora, or the manner in which a flora should be presented, given significant changes in technology and access to information, are changing rather dramatically, as recently expressed by Heywood (2001).

Some floras have both printed and online versions, the latter sometimes more updated (e.g., Flora Mesoamericana: <http://www.mobot.org/mobot/fm/welcome.html>), or with links to other floras and sites (e.g., Ecuador checklist, Jørgensen & León-Yánez, 1999; <http://www.mobot.org/mobot/research/ecuador/search.shtml>). Other floras or checklists are strictly online (Hassler & Swale, 2001).

A few organisations have, as their stated goal, the eventual inventory of all organisms on Earth. The magnitude of the problems - funding, organisational, and political - associated with getting such "big science" projects off the ground, coupled with insufficient numbers of specialists, seems almost insurmountable, and there is little hope that these efforts will have an impact in the near term. Two of the more prominent global initiatives are:

<http://www.species2000.org/> - Species 2000 has the objective of enumerating all known species of organisms on Earth (animals, plants, fungi and microbes) as the baseline dataset for studies of global biodiversity.

<http://www.all-species.org/> - The ALL Species Foundation is a non-profit organisation dedicated to the complete inventory of all species of life on Earth within the next 25 years.

A third broad regional undertaking is "The Inter-American Biodiversity Information Network", an initiative of the countries in the Americas to promote compatible means of collection, communication, and exchange of biodiversity information relevant to decision-making and education, using the Internet: <http://www.iabin-us.org/>

STATUS OF FERN FLORISTIC WORK, WITH EMPHASIS ON THE TROPICS AND SUBTROPICS

A spate of floristic work in the Neotropics in the last ten years has resulted in fern floras for Mexico (Mickel & Smith, 2004), Mesoamerica (Davidse et al., 1995), the Venezuelan Guayana (Smith, 1995), and Chile (Marticorena & Rodríguez, 1995), as well as annotated checklists for the Guianas (Boggan et al., 1997), Argentina (Zuloaga & Morrone, 1996), and Ecuador (Jørgensen & León-Yánez, 1999) (Fig. 1). In North America, the Mexican flora fills a sizeable gap between the United States and Central America, and this gives us relatively up-to-date floristic information spanning a continuous area from the arctic circle to the Colombian border (ca. 7° north latitude). For Mexico, we treat 1008 species, about a tenth of the world's total. This means that we now have reasonably up-to-date information on the occurrence and distribution of

nearly 1900 species, about 20% of the world's total, from Alaska and Canada to Panama. There are relatively recent and complete floras for Jamaica (Proctor, 1985), Puerto Rico (Proctor, 1989), the Lesser Antilles (Proctor, 1977), and the Bahamas (Correll & Correll, 1982). The Cuban flora (Greuter, 2003) is a work-in-progress, and Hispaniola needs a modern flora.

In South America, work has commenced on a conspectus or synoptical treatment of the pteridophytes of Bolivia, to include keys, diagnostic descriptions, illustrations, and maps (Kessler & Smith, in prep.). In the last eight years Kessler and collaborators have made 6000+ collections of Bolivian ferns and significantly added to our knowledge of pteridophytes from the southern Andes. We have published recently on 145 new records, species previously known from adjacent areas but unrecorded from Bolivia

Figure 1. Status of pteridophyte floras in Mesoamerica and South America. See Table 2 for references. ●Published floras. ▲Partial floras, checklists. ■Planned floras. △A few families done. ○State/District floras

Table 1. Numbers of species and numbers of endemics in some major pteridophyte floras of the world. Countries indicated by an asterisk, representing five continents and with relatively little overlap in species composition, include nearly 5000 spp., about half of the total fern species diversity in the world.

	No. spp.	No. endemics
FNANM	441	145
Mexico*	1008	186
Mesoamerica	1358	213
Venezuela	1204	
Peru	1060	130
Bolivia*	1160	
Chile	149	43
Europe	175	
Madagascar*	502	235
China*	c. 1600	
Philippines	1100	
Australia*	456	166

(Smith et al., 1999), and the number of new records has since grown. We now estimate about 1160 spp. from Bolivia, including 140 undescribed species. These additions suggest that Bolivia, which is at a phytogeographical crossroads, rivals other Andean floras in pteridophyte species richness. Heretofore, it has been the most poorly sampled country in Latin America. This increased knowledge will permit more accurate taxonomic and phytogeographic comparison with fern floras from adjacent areas, particularly Peru and Brazil. There is also a collaborative project underway between the Missouri Botanical Garden and several herbaria in Bolivia to produce an annotated catalogue of the vascular plants of Bolivia, employing the model used for the Ecuador checklist (Jørgensen & León-Yánez, 1999). A similar project is progressing in Venezuela to produce a catalogue of all vascular plants, and I have in late stages of preparation an updated Venezuelan fern flora (Smith, in prep.). Another recent flora, for a relatively large temperate area, is for Patagonia, Argentina (Correa, 1998).

The most conspicuous floristic gaps in our knowledge for the Neotropics are for Colombia, perhaps the richest of all tropical Latin American countries, and Brazil, also exceedingly rich, diverse, and the largest country in the Neotropics. A few fascicles for a fern flora of Colombia have been published (e.g., Arbeláez 1996, for Pteridaceae tribe Pterideae), but the task of a complete flora is formidable and unlikely to be completed anytime soon.

There are respectable or good floras for much of tropical and subtropical Africa (Fig. 2), especially for Southern Africa (most recently, Roux, 2001), but many of those for tropical Africa now need substantial updating to reflect increased collections, revised taxonomy, and new phylogenetic information. What is most needed is a comprehensive flora for all of tropical and subtropical Africa, and the relative paucity of ferns there makes this feasible. An initial attempt at this was begun by Schelpe (1969), but was never completed. Older floras for islands in the Indian Ocean, including Comoro Islands, Madagascar, Mascarenes, and Seychelles, were good for their time but are now significantly dated; Madagascar, in particular, needs a modern fern flora.

For tropical and subtropical Asia, floristic work lags behind other areas of the world (Fig. 3). A single volume has been produced for the Flora of Malesia in the last ten years (Kalkman & Nooteboom, 1998), and older volumes are now significantly dated. Even Holttum's (1954) Flora of Malaya, an exemplar 50 years ago, needs revision, and Copeland's (1958-1960) Philippine flora is even more seriously dated. New Guinea, Sumatra, Java, Borneo, and Sulawesi, among the most fern-rich areas of the world, all lack a modern flora. Regional floras exist for many states in India, several published within the last 10 years (see Table 1), but what is needed is a comprehensive modern flora for the entire Indian peninsula, a flora that takes into account material from Himalayan region, including Nepal, Bhutan, Myanmar, and Pakistan, as well as southwestern China. Myanmar is without a fern flora, and its ferns may be especially interesting because it is at the crossroads where four areas meet and the floras co-mingle: 1) India to the west; 2) China and the Himalayas to the north; 3) Vietnam,

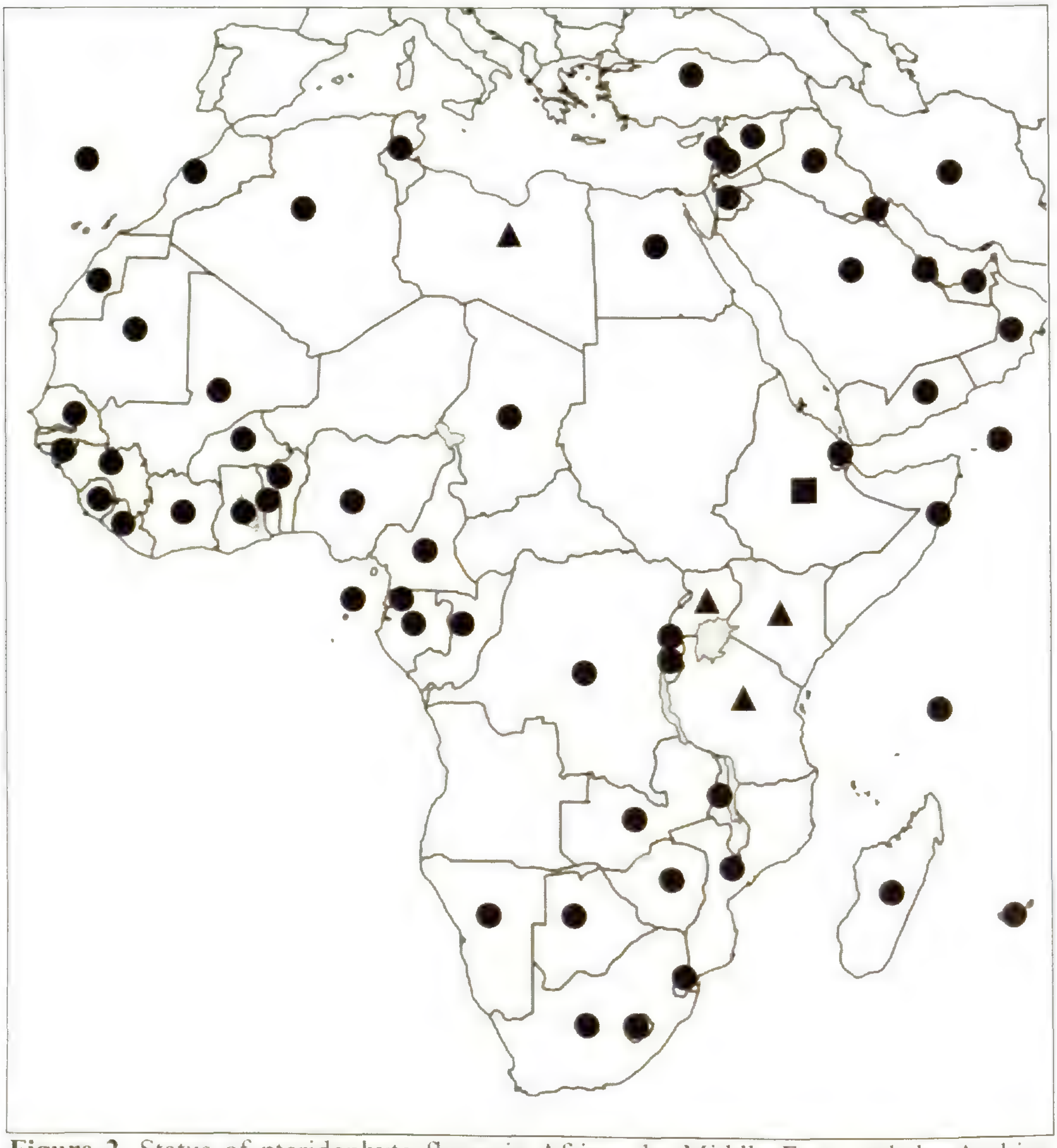

Figure 2. Status of pteridophyte floras in Africa, the Middle East, and the Arabian peninsula. See Table 2 for references. ●Published floras. ▲In progress. ■Partial floras.

Laos, Cambodia, and Thailand to the east; and 4) Malesia to the south. Bhutan, Laos, and Cambodia all lack a modern fern flora. Recent floras have been published for Assam (Borthakur et al., 2001) and Nepal (Thapa, 2002).

Floristic work in China has accelerated to the point that there is perhaps more effort being expended there than anywhere else in the world. Chinese language floras are available for many provinces, e.g., a flora of Guizhou (Wang & Wang, 2001). Seven volumes of the fern flora of China have been produced in the last five years (Chu, 1999; Kung, 2001; Lin, 2000; Shing, 1999, Wu Shiewhung, 1999a, 1999b; Wu Sugong, 2000), and a project is in the planning stages to produce an updated pteridophyte flora of China in English, with treatments being a collaboration between Chinese and non-Chinese specialists. As a preliminary working guide, "A pteridophyte checklist for China" has been assembled by Funston (2001). Some estimates suggest that the Sino/Himalayan pteridophyte flora encompasses 20% or more of extant ferns and allies. Such a figure is speculative, but there is no doubt that this area harbours an especially rich fern flora. The California Academy of Sciences, in collaboration with institutes in

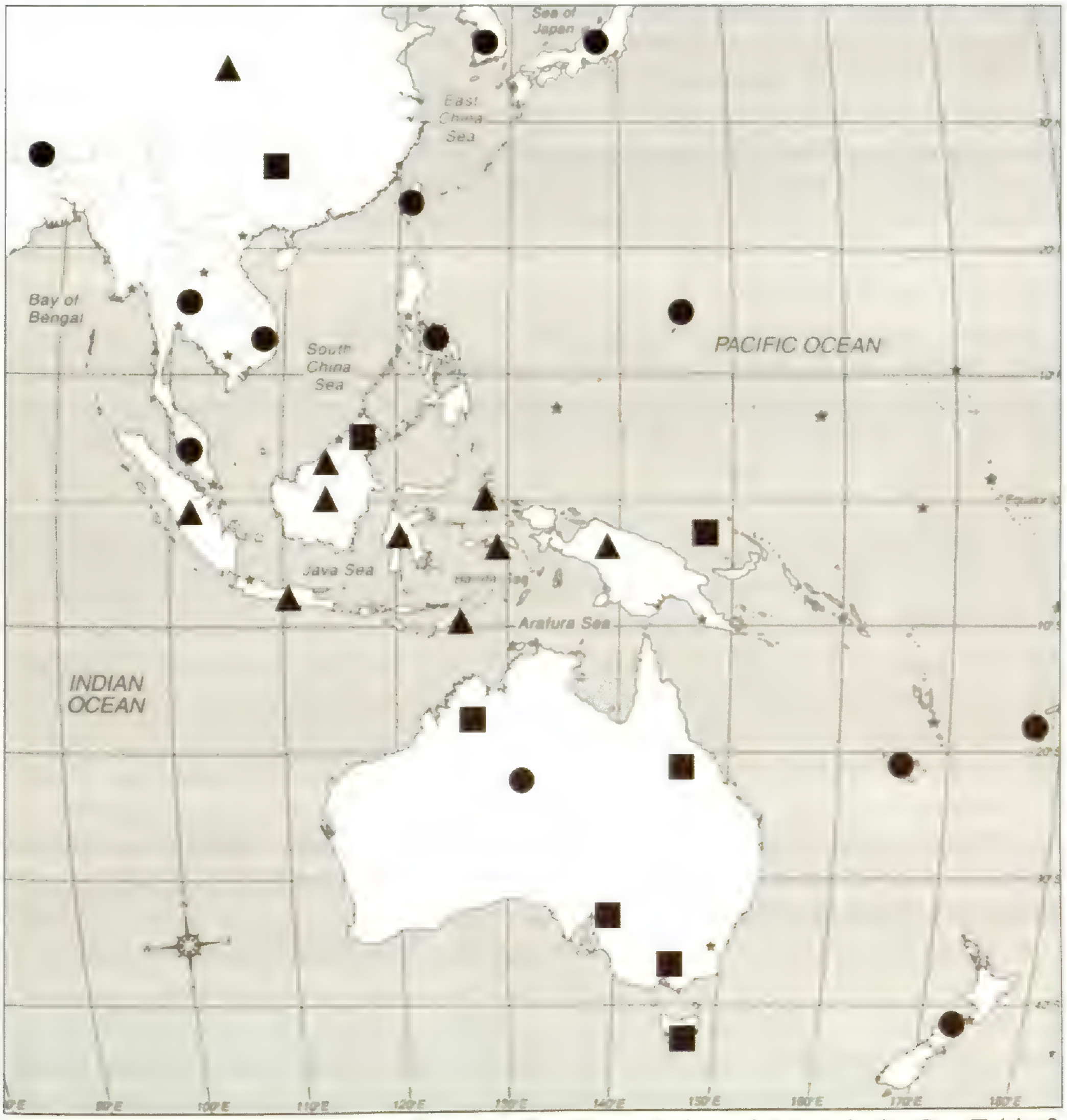

Figure 3. Status of pteridophyte floras in Southeast Asia and Australasia. See Table 2 for references. ●Published floras. ▲Partial floras. ■Florulas, state floras.

Kunming and other Chinese institutions, has an ambitious project to inventory the biota of Gaoligongshan Mountains in western Yunnan, near the border with Myanmar, one of the hottest of biodiversity "hotspots". Their online inventory of the pteridophytes, so far, indicates ca. 400 spp.: <http://research.calacademy.org/yunnan/>

Excellent, up-to-date floras exist for New Zealand (Brownsey & Smith-Dodsworth, 2001) and Australia (McCarthy, 1998), and for many states in the latter (most recently, Andrews, 1990; Garrett, 1996; Walsh & Entwisle, 1994). Hawaii also now has a recent flora (Palmer, 2003). Most critical needs in Australasia are for a comprehensive flora for all of Polynesia, integrating existing floras for individual islands or island groups and also requiring re-examination of related or same species from adjacent areas of Oceania, including Melanesia, Micronesia, as well as from Australia, New Zealand, and Malesia. In addition, we lack floras for the Solomon Islands, New Hebrides and Vanuatu Islands, and an updated flora for New Caledonia, containing one of the most fascinating and relictual floras, is highly desirable.

Some statistics for numbers of species in fern floras throughout the world are revealing (Table 1). Choosing five country-wide floras, one in each of the five continents (indicated by an asterisk in Table 1), we see that these countries, with relatively little overlap in species composition, include nearly 5000 spp., about half of the total fern species diversity in the world. Because of the more widespread nature of fern species compared to seed plant species (Smith, 1972), it is vitally important that floras be produced with wide context; hence my plea for an African tropical flora (continuing work begun by Schelpe, 1969), a broader Indian subcontinental flora, and an all-Polynesian flora.

The often long-attenuated act of producing a flora, the increase in collecting activities in tropical fern-rich areas, the discovery of undescribed species, changing species, generic, and family concepts, and the flood of new phylogenetic information virtually ensure that all floras of any complexity will be outdated to some extent by the time they are published, or quickly thereafter. Such recent tropical floras as for Peru (Tryon & Stolze, 1989a, 1989b, 1991, 1992, 1993, 1994), Madagascar (Christensen, 1932; Tardieu-Blot, 1951, 1952, 1958, 1960a, 1971), and Flora Malesiana (Holttum, 1963, 1982a, 1991; Holttum & Alston, 1959; Holttum & Hennipman, 1978; Kalkman & Nooteboom, 1998) already need significant revision, for many genera. Even the Flora of North America North of Mexico (Flora of North America Editorial Committee, 1993b), which is one of our more modern floras, and for a predominantly temperate area, is now dated in a number of aspects, with 10 newly described and 11 newly naturalized or previously overlooked species, adding 21 spp. to the total of 441 known in 1993; in addition, recircumscription of several families and genera is now warranted, e.g., Dennstaedtiaceae; Dryopteridaceae; Pteridaceae; *Asplenium*, *Cheilanthes*, *Polypodium*). None of this is a criticism of past works, merely a reflection of the massive amount of new information impacting circumscription and classification, and our ability to synthesize these data.

The existence, and inherent necessity, of partially completed floras is a fact of life, but frustrating for anyone trying to identify plants from many areas of the wet tropics and subtropics. It is quite likely that some floras will never be finished before advances in technology, more rapid means of presentation, and changing hypotheses about relationships and circumscription overtake them. The Flora of Ecuador is an example of an incomplete, long-ongoing flora, with the first fern fascicle produced in 1983 (Smith, 1983), and only five others produced since then (Harling & Andersson, 2001;

Øllgaard, 1988; Stolze, 1986; Stolze et al., 1994; Tryon, 1986), treating about 30% percent of the flora estimated to contain 1346 spp. (Jørgensen & León-Yánez, 1999). Of course, we can agree that even an outdated or incomplete flora is usually better than no flora at all!

The importance of florulas - floristic treatments for limited geographical areas - should not be underestimated or overlooked (Turner, 2001). They provide detailed insight to and understanding of the ferns of a small area, and they often reflect more intensive collecting activity. Consequently, they may provide more insight into species delimitation and hybridization than does a flora of a larger area. As Turner (2001) has commented, they often include important phytosociological data for ecologists and other scientists. Florulas can be especially useful for those interested in conservation or biogeographical analyses; they provide a basis for assessing historical changes in local floras; and they may encourage re-assessment of taxonomic problems. Some recent examples of neotropical florulas, sometimes including other vascular plants as well, include treatments for Barro Colorado Island (Croat, 1978); Guadalupe Island, Mexico (Moran, 1996); the region of Saint-Élie, French Guiana (Boudrie & Cremers, 2001), and Central French Guiana (Mori et al., 1997); Guaramacal National Park, Venezuela (Dorr et al., 2000); Reserva Maquipucuna, Ecuador (Webster & Rhode, 2001); Pico das Almas, Bahia, Brazil (Stannard, 1995); Reserva Ducke, near Manaus (Ribeiro et al., 1999); and Reservas Biológicas de Iquitos, Peru (Vasquez, 1997). The exceedingly rich flora of the Río Cenepa area in Amazonian Peru (Smith in Vásquez & van der Werff, in prep.) will document over 250 spp. of pteridophytes, including 7 new to science. Florulas can also be written for urban areas, and may be especially useful in tropical regions: notable examples are for Philippines (Zamora, 2000), Hong Kong (Edie, 1978) and Singapore (Johnson, 1977).

An idiosyncratic list of major pteridophyte floras, arranged by region and with emphasis on the most recent floras for a given area, is presented in Table 2. This list emphasizes larger, more comprehensive floras at the expense of small, local florulas. In addition, there is an intentional bias for floras from tropical and subtropical regions over floras from temperate regions. A fuller account of the floras of many temperate regions can often be found in comprehensive continental floras (e.g., for Flora Europaea area, Tutin et al., 1993: xxviii-xxx; Flora of Australia, McCarthy, 1998: 15-18), and a reasonably current account of the floras of the world can be obtained from Frodin (2001).

PHYLOGENETIC INFORMATION

Some might question whether it is appropriate to incorporate phylogenetic information in floras. However, for many users, floras are potentially the primary and perhaps easiest point of entry into the mushrooming phylogenetic literature of the last ten years. Phylogenetic information can also serve to inspire students and those just learning the plants of a given area, as well as educating a more general audience. Even if we choose not to accept particular phylogenetic hypotheses, we owe it to users to inform them of the growing body of evidence that supports our understanding of relationships, and the impact this has or may have on classification. Here are examples:

Higher Ranks. We now have solid evidence that 1) lycophytes form the sister group to all other vascular plant families, both ferns and seed plants, and that this separation occurred more than 350 million years ago, perhaps in the Devonian (Pryer et al., 2001,

Table 2. Floras and annotated checklists for pteridophytes, for major phytogeographic regions/countries of the world. References marked with an asterisk* are represented by symbols in Figures 1, 2, and 3.

NORTH AMERICA: **Bahamas** (Correll & Correll, 1982); **Canada** (Cody & Britton, 1989; FNA Ed. Comm., 1993b); **Costa Rica** (Grayum & Churchill, 1987; Lellinger, 1989); **Cuba** (Greuter, 2003; Sánchez, 2000); **Guatemala** (*Stolze, 1976, 1981, 1983); **Hispaniola** (Christensen, 1937); **Honduras** (*Nelson S. et al., 1996); **Jamaica** (Proctor, 1985); **Lesser Antilles** (Proctor, 1977); **Mesoamerica** (*Davidse et al., 1995); **Mexico** (Knobloch & Correll, 1962; Mickel, 1992; Mickel & Beitel, 1988; Mickel & Smith, 2004; Moran, 1996; Smith, 1981); **North America north of Mexico [Canada, Greenland, U.S.A.]** (FNA Ed. Comm., 1993b; Kartesz, 1994; Kartesz & Meacham, 1999; Lellinger, 1985); **Panama** (Lellinger, 1989); **Puerto Rico** (Proctor, 1989); **Trinidad-Tobago** (Baksh-Comeau, 2000; Mickel, 1985).

SOUTH AMERICA: **Argentina** (*Capurro, 1969; Correa, 1998; *de la Sota, 1972, 1973, *1977; *Moore, 1983; *Zuloaga & Morrone, 1996); **Bolivia** (Foster, 1958; *Kessler & Smith, in prep.; Kessler et al., 1999; Smith et al., 1999); **Brazil** (Angely, 1963; *Ribeiro et al., 1999; *Sehnem, 1967; Stannard, 1995; Tryon & Conant, 1975); **Chile** (Barrera, 1997; *Marticorena & Rodríguez, 1995); **Colombia** (*Arbeláez, 1996; Lellinger, 1989; *Murillo-A. & Murillo-P., 2003; *Murillo-P., 1988); **Ecuador** (Dodson & Gentry, 1978; *Jørgensen & León-Yánez, 1999; Harling & Andersson, 2001; Webster & Rhode, 2001); **Falkland Islands** (Broughton & McAdam, 2003; *Moore, 1968); **French Guiana** (Boudrie & Cremers, 2001; *Mori et al., 1997); **Galapagos Islands** (Lawesson et al., 1987; van der Werff, 1977; *Wiggins & Porter, 1971); **Guianas** (*Görts-van Rijn, 1994; *Boggan et al., 1997; <http://www.mnh.si.edu/biodiversity/bdg/planthtml/pterid.html>; **Paraguay** (Hassler, 1928; Peña-Chocarro et al., 1999); **Peru** (López Miranda, 1993; Tryon, 1964; *Tryon & Stolze, 1989a, 1989b, 1991, 1992, 1993, 1994; Vásquez, 1997; Young & León, 1990); **Suriname** (Kramer, 1978); **Uruguay** (*Legrand & Lombardo, 1958); **Venezuela** (*Dorr et al., 2000; *Smith, 1985; *Smith, 1995; Smith, in prep.; Steyermark & Huber, 1978; *Werff & Smith, 1980). **Paramo vegetation** (Luteyn, 1999).

EUROPE: (Jalas & Suominen, 1972; Øllgaard & Tind, 1988; Page, 1997; Pichi Sermolli, 1979; Tutin et al., 1993, with list of standard Europaean floras cited therein, pp. xxviii-xxx); **Azores** (Schäfer, 2001).

AFRICA (incl. Indian Ocean islands): **Algeria** (*Quézel & Santa, 1962); **Cameroon** (*Tardieu-Blot, 1964a); **Cape Verde Islands** (Lobin, 1998); **Djibouti** (*Andru, 1994; *Pichi Sermolli, 1954-1978, see under Ethiopia); **Egypt** (*Boulos, 1999-2002); **Equatorial Guinea [Annobón, Bioko, Río Muni]** (*Benl, 1978, 1980, 1982, 1988, 1991; Valayos et al., 2001); **Eritrea** (*Pichi Sermolli, 1954-1978, see under Ethiopia); **Ethiopia** (*Bizzari, 1975; *Pichi Sermolli, 1954, 1956, 1957, 1962, 1963a, 1963b, 1965, 1966, 1968,

1969a, 1969b, 1978); **French Intertropical Africa [Benin, Burkina Faso, Cameroon, Chad, Congo, Cote D'Ivoire, Guinea, Gabon, Senegal]** (*Tardieu-Blot, 1953; *Tardieu-Blot & Alston, 1957); **Gabon** (*Tardieu-Blot, 1964b); **Liberia** (*Harley, 1955); **Kenya** (Faden in Agnew, 1994); **Madagascar** (*Christensen, 1932; *Tardieu-Blot, 1951, 1952, 1958, 1960a, 1971); **Madeira** (*Press & Short, 1994); **Mascarene Isl.** (Badré & Cadet, 1978; Baker, 1877; Lorence, 1976, 1978; *Tardieu-Blot, 1960b); **Mauritania** (*Lebrun, 1998); **Mozambique** (*Schelpe & M. A. Diniz, 1979); **Prince Edward Islands (Marion Isl.)** (Alston & Schelpe, 1957); **Rwanda** (*Kornas et al., 1993); **Rwanda, Burundi, Kivu (Zaire)** (*Pichi Sermolli, 1983, 1985); **São Tomé/Principe** (*Alston, 1944; *Exell, 1959); **Seychelles** (Baker, 1877; *Tardieu-Blot, 1960b); **Socotra** (*Pichi Sermolli, 1954-1978, see under Ethiopia); **Somalia** (Pichi Sermolli, 1954-1978, see under Ethiopia; *Thulin, 1993); **Southern Africa [Botswana, Mozambique, Namibia, South Africa, Zimbabwe]** (*Burrows, 1990; Hancock & Lucas, 1973; *Jacobsen, 1983; *Roux, 2001; *Schelpe & Anthony, 1986); **Sudan** (Friis & Vollesen, 1998); **Swaziland** (*Roux, 2003); **Tanzania** (Schippers, 1993; **Tropical Africa** (Schelpe, 1969); **Tropical East Africa** (*Johns, 1991); **Tunisia** (*Cuénod et al., 1954); **Uganda** (Friis & Vollesen, 1998); **West Tropical Africa (Benin, Cameroon, Cote D'Ivoire, Fernando Po, Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Nigeria, Senegal, Sierra Leone, Togo**; *Alston, 1959); **Western Sahara** (*Lebrun, 1998); **Zambesiaca** (Botswana, Mozambique, Malawi, Zambia, Zimbabwe; *Schelpe, 1970; see also http://www.kew.org/efloras/); **Zambia** (*Kornas, 1979).

SW ASIA: **Arabian Peninsula [Bahrain, Kuwait, Oman, Qatar, Saudi Arabia, United Arab Emirates, Yemen]** (*Miller & Cope, 1996); **Iran** (*Parsa, 1950); **Iraq** (*Townsand & Guest, 1966); **Lebanon & Syria** (*Mouterde, 1963); **Middle East** (*Zohary et al., 1994); **Palestine** (Zohary, 1966); **Turkey** (*Davis, 1965).

ASIA: **China** (Boufford et al., undated; *Ching & Shing, 1990; *Chu, 1999; Edie, 1978; *Huang, 1994; Kitagawa, 1979; *Kung, 2001; *Lin, 2000; *Shing, 1999; *Wang & Wang, 2001; Wu Cheng-yih, 1983; *Wu Shiewhung, 1999a, 1999b; *Wu Sugong, 2000; *Yu & Li, 2001); **Eastern Himalaya [Bhutan, Darjeeling, Nepal, Sikkim]** (Hara, 1971; Iwatsuki, 1975); **India** (Baishyo & Rao, 1982; Bir, 1983; Borthakur et al., 2001; Chandra, 2000; Dhir, 1980; Dhir & Sood, 1981; Dixit, 1984, 1993; Dixit & Kumar, 2002; Ghosh et al., 2004; Jamir & Rao, 1988; Khullar, 1991, 1994; Manickam, 1986; Manicham & Irudayaraj, 1992, 2003; Mehra & Bir, 1964; Nayar & Geevarghese, 1993; H. Pande & P. Pande, 2002, 2003; P. Pande & H. Pande, 2002; Pullaiah et al., 2003; Singh & Panigrahi, 2004; Vasudeva & Bir, 1994; Verma et al., 1993); **Japan** (*Iwatsuki et al., 1995; Nakaike, 2004; Walker, 1976); **Korea** (*Park, 1975); **Mongolia** (Grubov, 1999a, 1999b); **Nepal** (Fraser-Jenkins, 1997; Gurung, 1991; Iwatsuki, 1988; *Thapa, 2002); **Pakistan** (Stewart, 1972); **Russia** (Fedorov, 1999, with list of other Russian floras cited therein, pp. 25-38; Komarov, 1968;

Krasnoborov, 2000; Tolmachev & Packer, 1995); **Sri Lanka** (Sledge, 1982).

SE ASIA: **Admiralty Islands** (*Wagner & Grether, 1948); **Malaysia** (*Holttum, 1954; *Parris et al., 1992; Parris & Latiff, 1997; Piggott, 1988; Turner, 1995); **Malesia [Indonesia, Malaysia, Singapore, Brunei Darussalam, the Philippines, Papua New Guinea in part]** (Beaman & Anderson, 1997; *Holttum, 1963, 1982a, 1991; *Holttum & Alston, 1959; *Holttum & Hennipman, 1978; *Kalkman & Nooteboom, 1998; *Kramer, 1971; *Parris et al., 1992; progress reviewed by Roos, 1996); **Philippines** (*Copeland, 1958-1960; Zamora, 2000); **Singapore** (Johnson, 1977); **Thailand** (*Tagawa & Iwatsuki, 1979-1989); **Vietnam** (Alston, 1951; *Pham-Hoàng, 1999); *Tardieu-Blot & Christensen, 1939-1951).

AUSTRALASIA: **Australia** (*Andrews, 1990; *Duncan & Isaac, 1986; *Garrett, 1996; Jones & Clemesha, 1980; *McCarthy, 1998; *Walsh & Entwisle, 1994; *Wheeler et al., 1992); **Kermadec Isl.** (Sykes, 1977); **Lord Howe, Norfolk Isls., and other Oceanic Islands** (Flora of Australia, 1993, 1994); **New Zealand** (*Brownsey & Smith-Dodsworth, 2001).

OCEANIA (incl. Melanesia, Polynesia, Micronesia, Mariana Isl.): **Cook Islands** (Game & Smith, in prep.); **Fiji** (*Brownlie, 1977); **Hawaii** (Palmer, 2003); **Mariana Isl.** (*Raulerson & Rinehart, 1992); **Micronesia** (Fosberg et al., 1982); **Moorea** (Murdock & Smith, 2003); **New Caledonia** (*Brownlie, 1969); **Ponape** (Glassman, 1952); **Rotuma** (St. John, 1954); **Samoa** (Christensen, 1943); **Society Islands** (Copeland, 1932); **Tonga** (Sykes, 1977).

2004b); 2) horsetails and whisk ferns (*Equisetum* and *Psilotum*, respectively), together with all ferns, form a clade called the monilophytes (Pryer et al., 2001, 2004b; Renzaglia et al., 2002); and that 3) the monilophytes are the sister group of the seed plants, including both flowering plants and gymnosperms (Pryer et al., 2001, 2004b). These and other studies suggest that our old concept of "pteridophytes", which once excluded both horsetails and whisk ferns from the fern clade, must be retired or modified. An alternative name for pteridophytes - "seed-free vascular plants" - has even been suggested (Pryer et al., 2002), to emphasize their phylogenetic position vis-à-vis extant seed plants. At the very least, modern floras should contain mention of studies that challenge our traditional classifications and our previously held understanding of relationships.

We ought to inform flora users of the now well-supported hypothesis of a sister relationship between the Psilotaceae and Ophioglossaceae (Manhart, 1995; Pryer et al., 2001, 2004b). Thus, Bierhorst (1968) appears to be vindicated in his hypothesis of a relationship between *Psilotum* and the ferns, but incorrect in postulating a close relationship to *Stromatopteris*, which is believed to be nested within Gleicheniaceae (Pryer et al., 2004b).

We need to reaffirm, in light of recent molecular evidence, that the leptosporangiate ferns (everything including and distal to Osmundaceae in the trees) are monophyletic (Pryer et al., 1995, 2001, 2004b). Further, we ought to inform users that Matoniaceae,

as well as Dipteridaceae and Cheiropleuriaceae, are closely related to Gleicheniaceae, which is in agreement with both morphological and molecular evidence; and that the schizaeoid ferns, including *Lygodium*, *Schizaea*, and *Anemia*, form a monophyletic group, also previously suspected. We owe it to consumers to emphasize the now strong evidence, contrary to most previously held opinions, that the heterosporous aquatic ferns, including Salviniaceae, Azollaceae, and Marsileaceae, are more closely related to one another than to any other fern groups (Hasebe et al., 1995; Pryer et al., 1995, 2001, 2004b).

We owe users reference to the phylogenetic literature that places several families whose relationships were previously problematic or contentious. The Plagiogyriaceae, Loxomataceae, and Hymenophyllopsidaceae appear to be allied to the tree ferns (Pryer et al., 2004b; Wolf et al., 1999) and together comprise a monophyletic "tree fern clade", even though some are not tree ferns at all, in stature! We assign this clade the rank Cyatheales, to emphasize their common origin, and it includes also the well known Cyatheaceae and Dicksoniaceae. We ought to be communicating this information in our floras, if for no other reason than to suggest politely that these hypotheses need further testing and re-interpretation of the traditional morphological evidence that allied them with families outside of the tree fern clade.

Lastly, molecular evidence strongly suggests that a large clade of higher leptosporangiate ferns is monophyletic and this clade comprises ca. 80% of all extant ferns. We can assign them the rank Polypodiales, again to emphasize their cohesiveness, apart from all other fern orders. This clade includes such diverse families as Dennstaedtiaceae, Aspleniaceae, Blechnaceae, Dryopteridaceae, Pteridaceae s.l. (with the included Vittariaceae and Parkeriaceae), Thelypteridaceae, Polypodiaceae (with the included Grammitidaceae), and other families (Pryer et al., 2001, 2004b). These families likely do not have separate origins from different sources among the basal leptosporangiate ferns, as most classifications and phylogenetic trees of the last 60 years have suggested (e.g., Bower, 1926; Pichi Sermolli, 1977; Holttum, 1973; Mickel, 1974; Wagner, 1969). Incorporation of this and other phylogenetic information into floras will go a long way toward educating the next generation of systematists and floristicians about the wealth of new data, and it will convey a sense of excitement and discovery about fern systematics to future generations.

Family Ranks. In addition to being pivotal in assessing higher level relationships, molecular data support recircumscription of several traditional families to conform to principles of monophyly. These include a more broadly defined Pteridaceae, to include Parkeriaceae, Vittariaceae and Adiantaceae (sister to each other), and Sinopteridaceae (Hasebe et al., 1995; Gastony & Rollo, 1995, 1998). Alternatively, Pteridaceae s.l. could be subdivided to include about five families (Cranfill & Schneider, 2004): Pteridaceae s.s. (*Pteris*, its immediate allies, the gymnogrammoid genera, e.g., *Pityrogramma*, *Eriosorus*, *Taenitis*); Parkeriaceae, comprising only *Acrostichum* and *Ceratopteris*; Cryptogrammaceae (including *Coniogramme*); Adiantaceae, including Adiantum and the Vittariaceae; and a large family Sinopteridaceae, containing various ill-defined cheilanthoid and pellaeoid genera. Several other families now also require redefinition to make them monophyletic, e.g., Dennstaedtiaceae (Hasebe et al., 1995; Wolf, 1995; Pryer et al., 2004b); Dryopteridaceae s.l. (Cranfill, unpubl. data); Athyriaceae; and Polypodiaceae (with Grammitidaceae nested within; Schneider et al., 2004a; Ranker et al., 2004).

Several problematic genera of previous uncertain relationship can now be placed with confidence in larger, recognized families. These include *Gymnogrammitis* (previously included in Davalliaceae or placed in its own family, Gymnogrammitidaceae; Schneider et al., 2002); and *Pleurosoriopsis* (previously in its own family or thought to be allied to Aspleniaceae or Pteridaceae). Both genera are now suspected of nesting within Polypodiaceae (Hasebe et al., 1995; Schneider et al., 2004a).

Generic Ranks. Numerous large classical genera are now believed to be paraphyletic or polyphyletic. Among these are *Asplenium*, from which numerous small segregate genera (e.g., *Diellia*, *Phyllitis*, *Loxoscaphe*, *Schaffneria*, *Ceterach*, *Camptosorus*) have been separated; all of these segregates appear to be nested within *Asplenium* (see Schneider et al., 2004c). The only segregate that has support from molecular studies is one that has most often been subsumed within *Asplenium* - the genus *Hymenasplenium* (Schneider et al., 2004b). Classical *Polypodium* is also polyphyletic, several times over (Schneider et al., 2004a), and should be restricted to the largely temperate *P. vulgare* group plus some allied species in Mexico, Mesoamerica, and northern South America. Simple-bladed *Grammitis* and pinnatifid *Ctenopteris* are likewise polyphyletic and need redefinition on some basis other than blade dissection, as classically construed (Ranker et al., 2004).

FLORAS OF THE FUTURE: RESOURCES, TOOLS, AND REFERENCES

What, then, should a modern flora, one borne in the 21st century, contain? Much of the basic information will be the same as in traditional floras. At a minimum, it is desirable to include descriptions or diagnoses of families, genera, and species; keys for their identification; accepted names and important synonymy; illustrations; maps or range statements; citation of representative specimens; and references. Descriptions need to be enlivened by remarking on interesting morphological features, characters often ignored or underutilized, e.g., aerophores and ventilation tissue, spore characters; chromosome numbers, gametophytic characters, fungal associates, and nectaries, as well as information about stipe and rhizome vasculature, leaf ptyxis, and blade architecture.

In addition, floras being planned or written today should strongly consider both online presentation and interactive keys.

1. Online Presentation. The advantages of producing a flora online are several; most importantly, this mode allows for floristic information to be readily updated. Examples of published pteridophyte floras with online versions include: *Flora of North America north of Mexico* (Flora of North America Editorial Committee, 1993b; <http://hua.huh.harvard.edu/FNA/>); *Flora Mesoamericana* (Davidse et al., 1995; <http://www.mobot.org/mobot/fm/welcome.html>); and *The Jepson manual: Higher plants of California* (<http://ucjeps.berkeley.edu/jepman.html>). An electronic pteridophyte flora for Australia is now available:
<http://www.anbg.gov.au/abrs/online-resources/flora/index.html

Checklists can also be put online; examples are Michael Hassler and Brian Swale's global checklist for pteridophytes: "Checklist of world ferns":
<http://homepages.caverock.net.nz/~bj/fern/>; and a site for Paramo plants, by Luteyn:
<http://www.botanypages.org/neill/paramos/site_intro.htm>. Many other checklists can be accessed through the Missouri Botanical Garden website:

<http://www.mobot.org/MOBOT/Research/alldb.shtml>

Local florulas are ideal candidates for online presentation. One example is "Ferns of the Canberra region", by Henry Kendall: <http://www.home.aone.net.au/byzantium/ferns/index.html>; another is for Wisconsin state, U.S.A.: <http://www.uwgb.edu/biodiversity/herbarium/pteridophytes/pteridophytes_of_wisconsin01.htm>; still another is a digital flora of Moorea (Society Islands): <http://ucjeps.berkeley.edu/moorea/pteridophytes.html>.

Rapid biological inventories (RBIs) also serve a purpose and are being increasingly employed when more detailed floras are either impractical or premature. They are often used to stimulate conservation action in threatened regions that are of high biological diversity and uniqueness. They are not intended as complete species lists, but may provide information on rare or unusual plants, range extensions, or habitats worthy of further exploration and collecting. A website that exhibits several sites in South America, one of which mentions important discoveries in the polypodiaceous genera *Solanopteris* and *Platycerium* (with image) and *Schizaea* in the Cordillera Azul in Peru (Depts. Loreto and San Martín), is: <http://fm2.fieldmuseum.org/rbi/results_bol01_dload.asp.>

A completely new kind of flora or interface is now being envisioned by systematists and ecologists in California. Called the PEGASUS database project, it seeks to integrate collection data with geographic, morphological, ecological, and phylogenetic data in a single relational database (Mishler, pers. comm.): <http://ucjeps.berkeley.edu/PEGASIS >

2. Interactive Keys. Interactive or multi-access keys are more user-friendly than traditional dichotomous keys because they allow the user to assess many characters, instead of only a few. Such keys are best displayed, and most easily used, in electronic form. A good example is Moran's key for neotropical pteridophyte genera, utilizing 87 morphological characters: <http://www.plantsystematics.org/>. Printed, multi-access keys are also possible, e.g., a key to *Grammitis* of New Guinea (Parris, 1983).

There are a great many other resources useful in preparation of floras today, resources that didn't exist ten years ago. Here are a few:

3. Indices. Several indices are essential tools for finding information about published names and types; these include: International Plant Names Index – IPNI <http://www.ipni.org/index.html>; Index Nominum Genericorum (Index to generic names) = ING <http://ravenel.si.edu/botany/ing/ingForm.cfm>; validly published suprageneric names, a site developed by Jim Reveal, at the University of Maryland <http://www.inform.umd.edu/PBIO/fam/sgindex.html>; TROPICOS database to plant names, places of publication, types, exsiccatae, maps, and other information <http://mobot.mobot.org/W3T/Search/vast.html>; Index to Herbaria, contacts, staff <http://www.nybg.org/bsci/ih/ih.html>

4. Types. Many herbaria have type information online, e.g., NY <http://sciweb.nybg.org/science2/VirtualHerbarium.asp>;
UC/JEPS <http://ucjeps.berkeley.edu/fern_types.html>;
US <http://ravenel.si.edu/botany/types/index.cfm>; and a consortium of herbaria in The Netherlands (Leiden, Utrecht, Wageningen) <http: www.nationaalherbarium.nl >; some of these sites also display images of types, e.g., MO, NY and US. In addition, some large, historically important collections can now be viewed online, e.g., the Linnaean Herbarium: <http://www.nhm.ac.uk/botany/linnaean databasehome.html>

5. Illustrations, Images. Line drawings by outstanding artists have become almost prohibitively expensive, but alternatives are available. Copyrighted illustrations can often be borrowed or scanned, with permission from the publisher or author. Herbarium

specimens can be photographed and the images digitized, making possible an infinite variety of illustrations, quickly and inexpensively. These range from habit photographs to details of indument and venation. Examples can be found on the Plant Systematics website: <http://www.plantsystematics.org/>; the Tropicos image Index <http://mobot.mobot.org/W3T/Search/image/imagefr.html>; the INBio website <http://darnis.inbio.ac.cr/ubis/>; and on individual websites <http://media.humboldt.edu/dkw1>

6. Maps And Atlases. Numerous websites are devoted to mapping, e.g., for Utah plants <http://www.nr.usu.edu/Geography-Department/utgeog/utvatlas/>; for New England ferns <http://neatlas.huh.harvard.edu/Pterid.html>. Published atlases exist for some temperate areas, e.g., Jalas & Suominen (1972) and Hultén and Fries (1986), but very few tropical ones.

Other sites provide base maps for countries of the world, e.g., <http://geography.usgs.gov/index.html>; <http://www.lib.utexas.edu/maps/map_sites/country_sites.html>; and <http://www.un.org/Depts/Cartographic/english/htmain.htm>

7. Glossaries. Many floras have glossaries of phytographical terms. A more comprehensive guide to botanical terminology, in four languages (English, French, Portuguese, and Spanish) is Lellinger (2002), and there are also downloadable dictionary files available in the Pteridologia section of the American Fern Society website: <http:/www.amerfernsoc.org>

Other Useful References For Floristic Work. This abbreviated list, arranged alphabetically, is intended only as a sample of sites often useful in conducting floristic work. They may be helpful in initiating further searches:

Bibliography. ePIC, Electronic Plant Information Centre, <http://www.kew.org/epic/>, is a project to bring together digitised information at Kew. The site can be used to obtain various kinds of information - bibliographies, nomenclators and checklists, publications and taxonomic works - as well as providing links to information from other organsations.

Chromosome Numbers. Information on chromosome numbers is available through standard indices (Goldblatt & Johnson, 2003, and preceding issues) or through at least two online sources: Index to chromosome numbers of Asian Pteridophyta <http://dapc.sci.kumamoto-u.ac.jp/pterid/topdb.html>; and Index to Plant Chromosome Numbers – IPNI <http://mobot.mobot.org/W3T/Search/ipcn.html>

Classifications. Classificatory information can be gleaned from a few websites, e.g., Hassler and Swale's global "Checklist of world ferns" <http://homepages.caverock.net.nz/~bj/fern/>; standard references can be consulted for more detailed information, e.g., Kubitzki (1990); Tryon & Tryon (1982).

Conservation. Floras have a role in providing data related to conservation issues, i.e., preparation of Red Data List assessment (see Golding & Smith, 2001). A symposium (Fern Flora Worldwide: Threats and Responses) dealing primarily with fern conservation was sponsored by the British Pteridological Society in 2001, and later published (Dyer et al., 2002; see also <http://www.nhm.ac.uk/hosted_sites/bps/symposium/symposiumcontents.htm>)

The major conservation website is: 2003 IUCN Red List of Threatened Species <http://www.redlist.org/>; for the United States <http://ecos.fws.gov/tess_public/TESSWebpageVipListed?code=N&listings=0>; additional conservation sites exist for many countries and regions within countries.

Dictionaries. A dictionary of botanical epithets:
<http://www.winternet.com/~chuckg/dictionary.html>
Ecological Research Sites. Long term ecological research sites (LTER sites): <http://lternet.edu/sites/>
Exsiccatae. Specimen citations (exsiccatae) are an integral part of floras, documenting the existence of a given taxon in specific region. Examples are to be found in Berry et al., 1995; Davidse et al., 1995; Holttum, 1982b, Mickel & Smith, 2004; see also under Indices, TROPICOS. Collection data for California plants can be obtained from: <http://www.mip.berkeley.edu/www_apps/smasch/>
Fossil Information/Geological Timeline. Recent comprehensive references, all published, are: Collinson, 1996, 2001; Galtier & Phillips, 1996; Pryer et al., 2004b; Skog, 2001.
Gazetteers. <http://www.calle.com/world/>
Genera. Websites for specific genera, e.g., the *Elaphoglossum* homepage, by Moran et al.: <http://www.nybg.org/bsci/res/moran/elaphoglossum.html>
Invasive Ferns. *Salvinia molesta:* <http://salvinia.er.usgs.gov/>
Living Material. Many botanical gardens have their own website from which lists of living plants, and sometimes images, can be obtained, e.g., the University of California Botanical Garden: <http://botanicalgarden.berkeley.edu/>; and the University of Connecticut: <http://florawww.eeb.uconn.edu/>
One site allows searches of multiple botanical gardens at the same time:
<http://rbg-web2.rbge.org.uk/forms/multisite2.html>
Nomenclators: e.g., a list of *Polystichum* spp. (Barrington):
<http://www.uvm.edu/~dbarring/polystichum/>
Nomenclature. International Code of Botanical Nomenclature:
<http://www.bgbm.fu-berlin.de/iapt/nomenclature/code/SaintLouis/0000St.Luistitle.htm>
An issue that may impact floras of the future is the nomenclatural system to be used. The Phylocode, now being argued and written, is an attempt to de-emphasize ranks and establish a system for the names of clades, a rank-free system of names. For history and literature, see: <http://www.ohiou.edu/phylocode/>
Paleogeographic Maps: The juxtaposition of the continents, through time, can be viewed on several paleogeographic websites:
<http://pgap.uchicago.edu/global290-0pgeogrev.mov>; <http://pgap.uchicago.edu/>; <http://www.scotese.com/>
Phylogenetic Trees And Other Related Information: Phylogenetic trees are found on several websites, including the following: Tree of Life
<http://tolweb.org/tree?group=leptosporangiate_ferns&contgroup=Filicopsida>; and TreeBase, a database of knowledge about phylogenetic trees
<http://www.treebase.org/treebase/>
For various phylogenetic projects in which I have been involved, there is a database to record DNA voucher information, tissue availability, sequence information, and references (Fern DNA database): <http://www.biology.duke.edu/pryerlab/ferndb/index.html>
Societies. American Fern Society <http://amerfernsoc.org/>; and British Pteridological Society <http://www.nhm.ac.uk/hosted_sites/bps/>

PROBLEMS

The preparation of floras and florulas is not without difficulty. Training of individuals to conduct floristic work languishes in Europe and the United States. In the U.S., within

the last ten years, pteridologists and pteridological positions have been lost at the Field Museum in Chicago; University of Michigan; Gray Herbarium, Harvard University; Missouri Botanical Garden; and Smithsonian Institution. These institutions hold five of the seven largest research collections of pteridophytes in the United States. The loss of mentors leads soon to the loss of students. Students in more developed countries often must confine themselves to projects having a phylogenetic focus in order to make themselves marketable, and consequently lack sufficient training to execute traditional or modern floristic work. Funding agencies do not always look favourably upon efforts to produce modern floras.

Problems of a political nature also impede progress in floristic work in particular and systematics in general. For example, Colombian botanists are now unable to send duplicates-for-identification to specialists outside of the country. The cost of collection permits has also become prohibitively expensive in some areas. Some areas of the globe are unsafe for fieldwork and plant collecting.

In summary, there is a critical lack of people able to invest the time, facility, and incentive to carry out modern floristic work. In addition, the foundation for any modern flora is monography, and few monographs are being written. This requires that modern floras, at least for wet tropical areas, be almost semi-monographic, in that species delimitations and relationships be explored in a broader context, with consideration of material outside the flora boundaries. It is clear that the next generation of floras must have the full participation of individuals in those countries with the richest floras, i.e., systematists in the wet tropics. And this is the conundrum, because the resources for doing floristic work, especially access to large, historically important herbaria, types, and libraries, are often inadequate in the very countries where they are most needed.

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THE PTERIDOPHYTIC DIVERSITY IN THE CLOUD MONTANE FORESTS FROM SALTA, NW ARGENTINA

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The area, phytogeographically called 'Yungas', covers a large part of Northwestern Argentina in Salta, Jujuy, Tucumán and Catamarca provinces. In these forests, ranging from 400-3,000m altitude, low clouds and mists are almost permanent, with an annual rainfall reaching 3,000 mm. The Province of Salta, between 22º-26º20´S, 62º20´-68º50´ W, has a surface area of 154,775 km^2, half the size of the Province of Buenos Aires, the largest state of Argentina. The 'Yungas' occur from north to south along the Subandean Mountains and the Eastern Range of the Andes. In Argentina, 86 genera and 346 native taxa of ferns and allied plants are recorded. Of these, 52 genera and 133 species are reported for Salta. The local high humidity and the physiography have promoted the development of an exuberant vegetation, with large and old trees and abundant mosses and epiphytic plants. In this peculiar habitat ferns such as Asplenium achalense Hieron., A. auritum Sw., Lellingeria tungurahue (Rosenst.) A.R. Sm. & R.C. Moran, Microgramma squamulosa (Kaulf.) de la Sota, Pecluma filicula (Kaulf.) G.M. Price, P. oranense de la Sota, Polytaenium lineatum (Sw.) J.E.Sm., Phlebodium pseudoaureum (Cav.) Lellinger and others, are found. Also large terrestrial or epipetric ferns including species of Alsophila, Blechnum (sect. Lomariocycas) and Megalastrum are recorded. The few taxa of Botrychium and Ophioglossum are uncommon and Huperzia mandiocana (Raddi) Trevis., H. subulata and Psilotum nudum (L.) P. Beauv. are rare in the epiphytic communities; all these species require protection.

NOTEWORTHY FERN DISCOVERIES IN THE PHILIPPINES AT THE TURN OF THE 21ST CENTURY

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Key words: *Aglaomorpha cornucopia*, Bohol, conservation, *Ctenitis humilis*, *Cyrtomium*, *Dennstaedtia macgregori*, ferns, Kalinga, Luzon, Mt. Bali-it, Mt. Banahaw, pteridophytes, Rajah Sikatuna Protected Landscape, Wildlife Resources Conservation and Protection Act

ABSTRACT

The status of pteridological research in the Philippines at the turn of the 21st century is presented and discussed. An electronic database containing collection and taxonomic information on nearly 23,000 collection numbers of Philippine pteridophyte specimens in herbaria around the world was started in 1994, a collaborative personal and institutional endeavor. I also provide a synthesis of the results of my field explorations in three protected areas in the last three years. Noteworthy of these are the rediscovery and confirmation of the presence in the Philippines of the genus *Cyrtomium*, and the rediscovery of *Aglaomorpha cornucopia*, *Antrophyum williamsii*, *Ctenitis humilis*, and *Dennstaedtia macgregori*, rare Philippine endemics. The need for extensive botanical explorations in the Philippines is imperative for our understanding of biodiversity and sound conservation management. The implications for scientific research and cooperation of current laws regarding biological collection and transport, especially the Wildlife Resources Conservation and Protection Act, are also presented.

INTRODUCTION

The last decade of the 20th century, though seemingly quiescent, was a period of rather active data repatriation for Philippine pteridology. In 1994, I started an electronic database of herbarium label data with the fern collections at F, MU, and US in the United States and BM and K in England. Subsequently, I incorporated the paper database of herbarium materials collected and annotated examined by M. G. Price since the late 1960s that comprise nearly 30% of the records. Pteridological collections of L. L. Co (at PUH) between 1970 and 1993 likewise make up an additional 5% of the total records. In addition, Philippine materials cited in literature that we have not seen yet were also noted. With nearly 23,000 records/collection numbers, this electronic database contains herbarium data of more than 90% of the pre-World War II collections and some 70-80% of the post-World War II collections of Philippine ferns and fern allies and includes all of my own collections from 1989 to 2004. I have singlehandedly prepared this database, hence data quality, if ever compromised, has been at a minimum. This may indeed be the most powerful resource for Philippine pteridological collection data to date. However, databasing of Philippine fern collection deposited in

major Asian (BO and SING) and European herbaria (B, MA, BM, K, E, and L) is far from substantial. For instance, only Selaginellaceae and Lycopodiaceae in both BM and K were included in the database. Initial data suggest that in *Selaginella* alone, nearly 5% and 12% at K and BM, respectively, are unique, i.e. I have not seen replicates in other herbaria. A day of databasing effort at E has resulted in 221 numbers; about 33% of these are unique. I have never visited B, MA, and L and, except for those materials cited in literature, I have not included any of their accessioned Philippine pteridophytes.

The turn of the 21st century has been marked by a series of pteridological explorations in Bohol and Luzon (2002-2004). These explorations have greatly increased our meagre understanding of the richness of the pteridophyte flora of the heavily botanised Mt. Banahaw in Luzon and the less-explored karst forests of Bohol and montane forests of Luzon's Central Cordillera.

In this study, I provide a synthesis of our pteridological explorations in Rajah Sikatuna Protected Landscape (RSPL) and adjacent areas in Bohol, Mt. Banahaw mountain complex and Mt. Bali-it, Balbalasang-Balbalan National Park (BBNP) in Luzon (Barcelona, 2003). I also evaluate the collection and conservation status of rare Philippine endemic pteridophytes, especially those only known from types or from very few collections. I further explore alternatives to sound planning of future pteridological explorations and conservation management. More importantly, I discuss the implications to scientific research of the current laws regarding collection and transport of biological specimens.

MATERIALS AND METHODS

I am providing a synthesis of the results of the fern collecting explorations that we

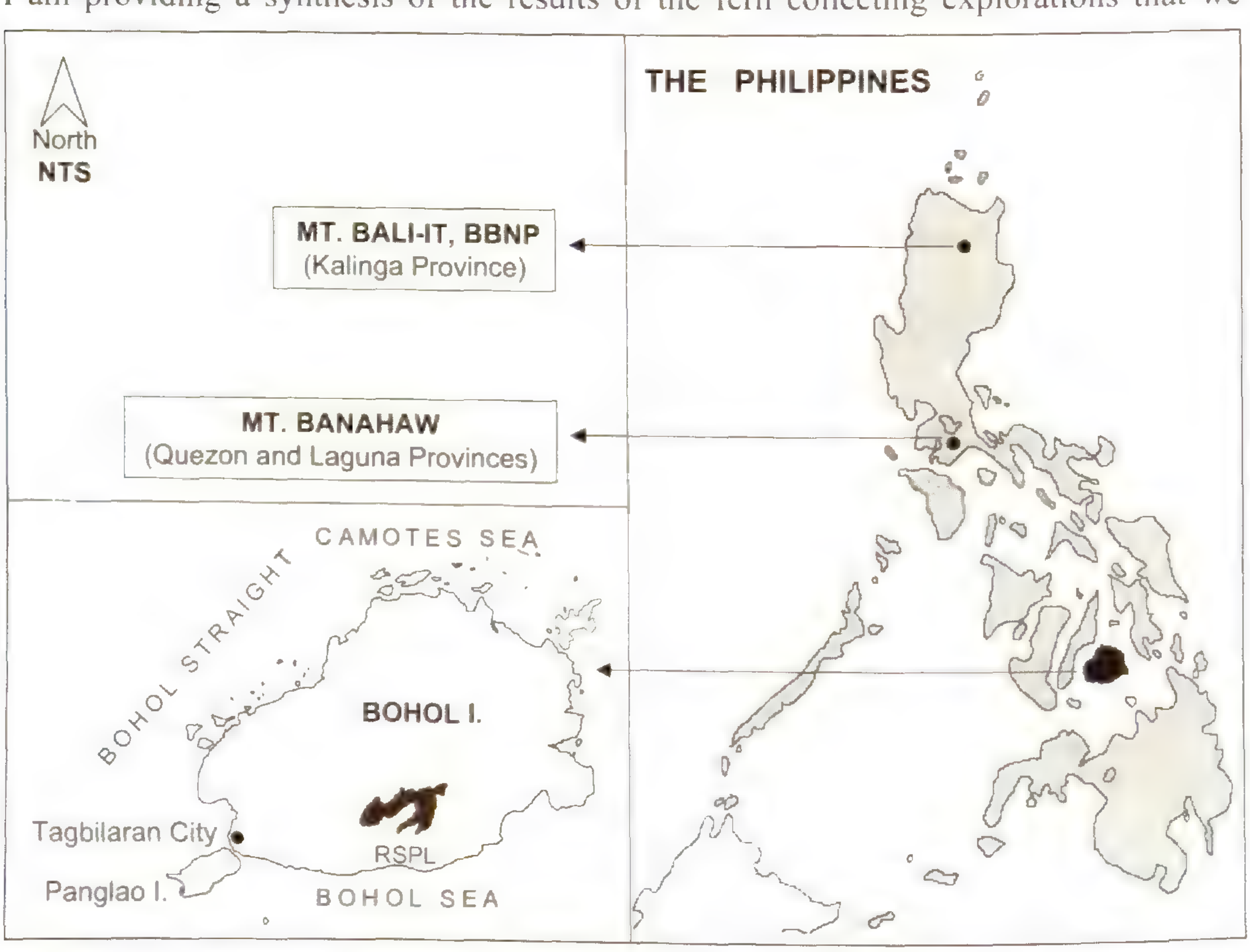

Figure 1. Location map of recent pteridological collecting localities in the Philippines (2002-2004).

conducted in three protected areas, namely Mt. Banahaw mountain complex that straddles Quezon and Laguna Provinces: Oct. 16-25, 2002 (Barangay Laló, Tayabas approach), Mar. 27-Apr. 6, 2003 (Lucban Cone), and Sept. 9-21, 2003 (Barangay Kinabuhayan, Dolores approach); Mt. Bali-it, Balbalasang-Balbalan National Park (BBNP), Kalinga Province on Feb. 16 to Mar. 3, 2003; and Bohol Island particularly within the Rajah Sikatunah Protected Landscape (RSPL) and vicinity on Nov. 18-22, 2003 and Jan. 16-Feb. 12, 2004 (Fig. 1). Exact collection localities in BBNP and RSPL are provided in Barcelona (2003) and Barcelona et al. (*in press*), respectively. All collections are currently deposited at the PNH.

RESULTS

BOHOL ISLAND [Rajah Sikatuna Protected Landscape (RSPL) and vicinity]

Our recent collecting explorations in the island of Bohol, particularly within and in the vicinity of RSPL resulted in a total of 170 species in 63 genera and 28 families reported for the island since 1841, 92 species of which are our new additions (Barcelona et al., *in press*). Noteworthy of these are the collections of *Pteris whitfordii* Copel., *Antrophyum williamsii* Benedict, *Drynaria descensa* Copel., and *Lomagramma merrillii* Holtt., confirming range extentions of these disjunct Philippine endemics. We also re-collected *Ctenitis humilis* Holtt., a local endemic first reported for the Philippines by a collection from Bohol (*Ramos BS43032*) in 1923 and subsequently collected from Mindoro (*Bartlett 13626*) in 1935. A population of *C. humilis* in RSPL was recently found along a riverbank. It was in the limestone forests of RSPL that I first encountered wild populations of the staghorn, *Platycerium coronarium* (König. ex Müller) Desv. Fifteen previously reported species in Bohol have not been re-collected.

LUZON: Kalinga Province, Balbalasang-balbalan Natural Park (BBNP)

I have previously reported (Barcelona, 2003) on the preliminary results of a fern collecting expedition to Mt. Bali-it, Balbalasang-Balbalan National Park (BBNP) in 2002. In a little less than 3 weeks, we collected 167 species in 67 genera and 30 families. Sampling of such a narrow strip of Luzon's Central Cordillera forest from the heavily disturbed areas at ca. 950m to the more or less pristine upper montane forest at 2,217m has yielded an amazingly rich pteridophyte flora. BBNP is home to nearly 15% of the total species of ferns and fern allies reported for the Philippines. 16 species and two varieties are country endemics, 4 of which are restricted to Luzon's Central Cordillera. During this fieldwork, we rediscovered fertile plants of *Cyrtomium* (= *Phanerophlebia* in Copeland's flora) confirming the presence of this genus in the Philippines, particularly the northern portion of Luzon's Central Cordillera (Fig. 2a & b). Previous reports of *Cyrtomium* in the Philippines were based on a sterile collection, *Mearns 38* (US), from Mt. Sto. Tomas in Benguet Province in 1905 and on that of Loher from Mt. Data (ca. 2,250m) at the turn of the 19th century reported by Christ (Copeland, 1960). Shing (1982) annotated *Mearns 38* as *Cyrtomium micropteron* (Kunze) Ching. We still have to see Loher's collection. The correct taxonomic identity of *Mearns 38* and of our recent collections (Barcelona *1838* and *1856*) still needs to be reevaluated. Gross morphological differences, however, strongly suggest that there are at least two species of *Cyrtomium* in the Philippines. Mei-lu and Cheng's (2003) recent paper on the distribution of this genus reports its range to extend only as far south as Taiwan in Southeast Asia. On Mt. Bali-it, *Cyrtomium* is infrequent, growing in moist gulleys of dry, mossy, closed-canopy forests between 1940-1960m (Barcelona, 2003). These

rediscoveries indicate that the more or less pristine montane forests of northern Luzon may still indeed contain genetic resources of endemic plants whose conservation status remains poorly known due to deficient collection and ecological data.

We also discovered patches of *Aglaomorpha cornucopia* (= *Thayeria cornucopia*), exclusively dominating the ground cover in some areas of Mt. Bali-it's upper montane forests at elevations between 1700-2130m. The current conservation status of *A. cornucopia* is *rare* (IUCN, 1997). Likewise, we also rediscovered a population of *Dennstaedtia macgregori* Copel., a Philippine endemic fern known only from a single collection (the type) from Mt. Polis in 1913, (*MacGregor BS19768* - holotype: MICH; isotype: US). On Mt. Bali-it, plants of *D. macgregori* were found growing in moist gulleys of the closed-canopy forest interior at ca. 1700m. A third specimen, *Iwatsuki, K. et al. P-533* at PNH (perhaps distributed as *D. hooveri*), has been positively identified as *D. macgregori*. It was collected in Ilocos Norte Province, also in northern Luzon, in the Mt. Sicapoa range at ca. 1600m in 1975. This endemic fern may indeed be more widely distributed in Luzon than the current meagre collection data suggest.

LUZON: Laguna and Quezon Provinces , Mt. Banahaw

Preliminary evaluation of database information on pteridophytes collected/reported

Figure 2a. *Cyrtomium* cf. *fortunei* J. Sm.

from Mt. Banahaw since 1870 (by Weiss) up to our own series of explorations in 2002-2003 provides an estimated total of 312 species in 87 genera and 29 families. These are the results of prolific collecting activities (not less than 60 collecting trips) on different slopes of this area for two centuries. This richness is comparable to the pteridophyte flora of the adjacent Mt. Makiling in Laguna and Batangas Provinces (305 spp.) (Price, 1975). Due to their proximity to Manila and therefore their accessibility, the Mt. Banahaw mountain complex (including Lucban Cone) and Mt. Makiling in Luzon are the two most heavily botanised areas in the Philippines with readily comparable collection intensities. Each harbours nearly 30 % of the country's known pteridophyte species. A detailed account of the pteridophyte flora of Mt. Banahaw will be published separately.

DISCUSSION

The island of Bohol is one of the few areas in the Philippines that supports a vegetation unique to the karst limestone habitats. For a long period of time, this island has been very poorly known botanically until our recent explorations in 2003 and 2004 (Barcelona et al., *in press*). In the last century and a half, the total number of pteridophyte collections, for instance, is only a little more than 100 numbers representing about 74 species. These were results of early explorations from that of Cuming in1841, McGregor in 1906 and 1910, Bartsch in 1908, and Ramos in 1923. More than 80% of the pteridophytes currently deposited in herbaria around the world from Bohol were collected by Maximo Ramos, a prolific Filipino plant collector and staff member of the then Bureau of Science herbarium (now Philippine National Herbarium) who collected in Bilar, Dimiao, Sevilla, and Valencia. It was not until nearly half a century later that Konyo and Edaño (1957) and Co (who collected in Dagohoy, Danao, Inabanga & Pilar in 1995) added more materials to these meagre historical collections.

The total destruction of the Bureau of Science herbarium during World War II

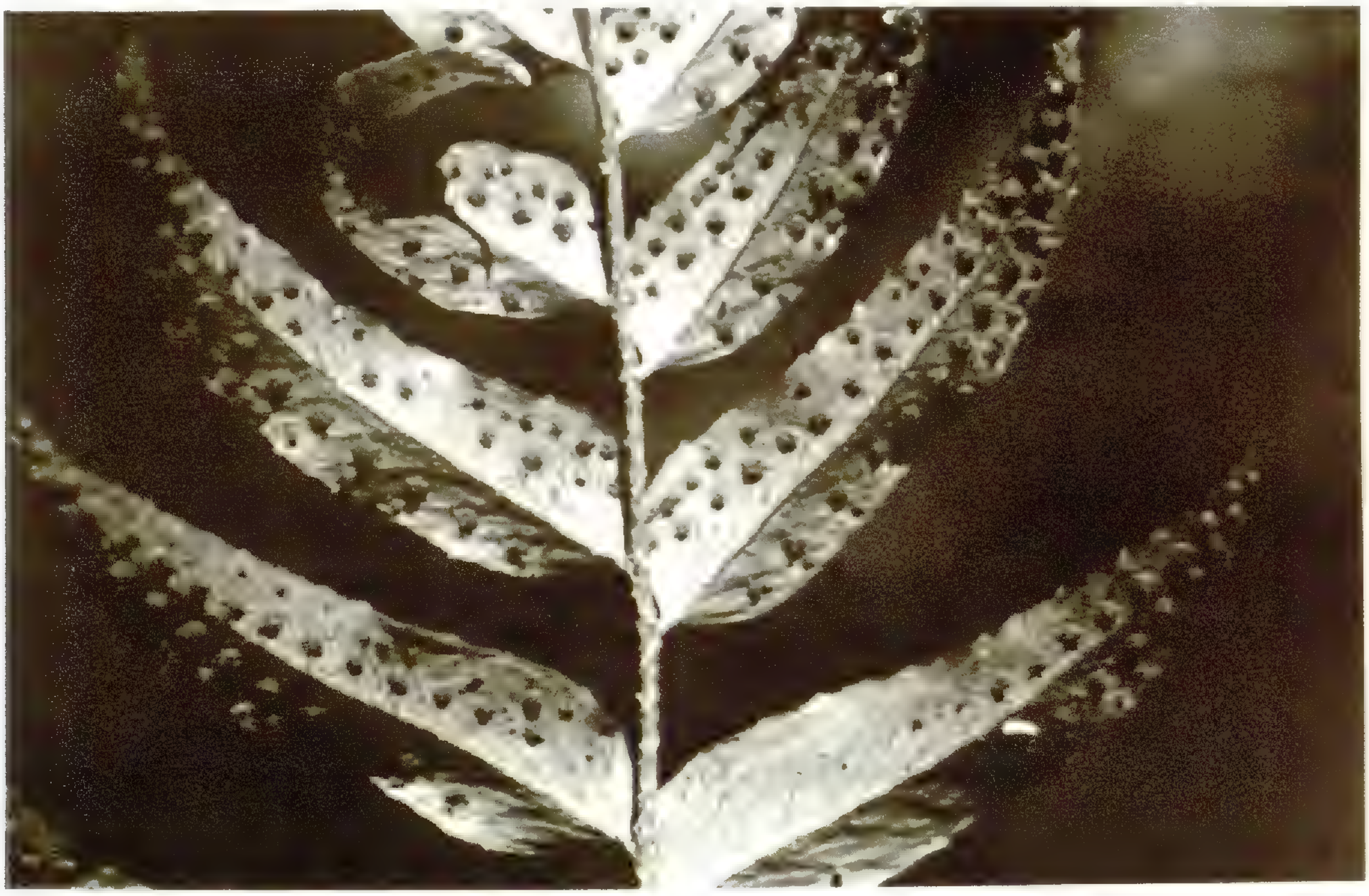

Figure 2b. *Cyrtomium* cf. *fortunei* J. Sm.

consequently left the Philippines devoid of any pre-war botanical collections. After the war, herbaria in Europe, Asia, and the United States, repatriated a substantial number of herbarium specimens to form the core collection of the Philippine National Herbarium. Until our collecting expedition last year, only one specimen, *Selaginella llanosii* Hieron. (*Ramos BS43014*) from Bohol was included in the accessioned pteridophyte collections of the PNH. Co's collections are deposited at PUH.

Despite the rich pteridological collections from Mt. Banahaw, there was virtually no published study on this plant group until recently (Banaticla and Buot, 2004). This ecological study along an altitudinal gradient on Lucban Cone reported 93 species of pteridophytes in 47 genera and 24 families. This number represents approximately 52% of the total species reported for Lucban Cone and vicinity (Barcelona, unpublished) and approximately 30% of those reported for the entire Banahaw mountain complex to date.

Results of our recent pteridological explorations in Luzon and Bohol strongly suggest that there still is a great need for botanical exploration in the Philippines. Though perhaps the most complete single resource of collection and taxonomic information on any plant group in the country, our current data cannot be used to assess meaningfully the distribution range and conservation status of important taxa, especially endemics. Unless substantiated by more or less equal collection intensity in time and effort relative to land area, species lists on a mountain/regional/island basis are meaningless and non-conclusive when compared and interpreted beyond what they intend to convey, species lists at a particular time and place. If public education is important in conservation, I believe that serious field exploration of botanically important areas (especially protected areas) is equally important. Raising public awareness of our country's biodiversity must be done simultaneously with extensive (and intensive) biological collections. When resources are limited (time, manpower, and money), it is more rational, in my opinion, to prioritise extensive collection over ecological surveys concentrated on a particular mountain slope, for instance. It is only through this endeavor that novel taxa can potentially be discovered and the real conservation status of endemics can be meaningfully assessed.

The Philippines is among the first countries to have drafted and implemented regulatory laws regarding the collection and transport of biological resources. The Wildlife Resources Conservation and Protection Act (Republic Act No. 9147, signed in 2001) and its precursor, Executive Order 247 of 1997, have been both a boon and a bane to conservation. Despite the noble intentions of preventing biological piracy, poaching of wildlife for trade, and illegal logging, and promoting respect and recognition of intellectual property rights, especially of indigenous groups, the Wildlife Act has serious negative implications for research, conservation, and the preservation of Filipino heritage. Certain provisions of the act severely hamper collaborative field explorations among biologists. For example, it has made the exchange of replicate biological specimens between museums and scientific institutions around the world nearly impossible. Without such cooperative pre-World War II exchanges and the subsequent repatriation of specimens after the war, our museums would be nearly devoid of historical biological specimens. The current conflicts between the provisions of the Wildlife Act and other Republic Acts (e.g. the National Museum Act of 1998, RA8492 and Indigenous People's Rights Act of 1997, RA 8371) have caused confusion in implementation and have blurred the mandates of different government agencies in the Philippines. The extensive red tape associated with obtaining collecting permits for scientific purposes has disadvantaged Filipino scientists (especially those working for

the government) relative to their foreign counterparts, in no small measure due to funding problems. While our forest resources are lost by the minute, Filipino biologists are forced to wait months or even years to obtain collecting permits. It is in our best national interest to undertake a serious review of the Wildlife Act and its subsequent amendments. It is imperative that we reflect upon our ultimate goals for conservation in the Philippines. In doing so, we need to understand the role of scientific study in assessing and understanding not only the extent of our biodiversity, but also the causes of its imperilment. Science and conservation are not antagonistic and in fact conservation can only be done in a meaningful way with a strong scientific rationale and understanding. Conservations decrees need to be written with an understanding of the role of science and should accommodate and promote the scientific study of our biological heritage.

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MOLECULAR PHYLOGENETIC STUDY ON DAVALLIACEAE

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Key words: Davalliaceae, molecular phylogeny, *atpB*, *rbcL*, *accD*, *atpB-rbcL* spacer, *rbcL-accD* spacer, intrafamilial relationship

ABSTRACT

In previous classifications based on morphological characters, Davalliaceae comprises from four to ten genera, whose concepts differ among authors. This study analyzed a molecular phylogeny of 36 species in five genera. Deduced phylogenetic relationships based on a combined dataset of five continuous chloroplast regions, *atpB*, *rbcL*, *accD*, *atpB-rbcL* spacer, and *rbcL-accD* spacer, are incongruent to any previous classifications, and none of the genera are monophyletic. *Araiostegia* is divided to two clades, one of which is the most basal and includes *Davallodes*, and the other is nested within the rest of the family. *Davallia* is divided into three clades, in accordance with three sections classified mainly by scale morphologies, and the clades are separated by the intervention of a clade of *Araiostegia*, *Humata* and *Scyphularia*. *Humata* and *Scyphularia* are also paraphyletic.

INTRODUCTION

Davalliaceae is an epiphytic leptosporangiate fern family. Most species are distributed in the humid tropics of Asia, Australasia, and the Pacific islands, and a few others occur in Europe, Africa and nearby islands. Phylogenetic studies showed that Davalliaceae, along with polygrammoid ferns (Polypodiaceae and Grammitidaceae) (Schneider et al., 2004a), form a monophyletic epiphytic clade, which is together sister to oleandroid ferns (Hasebe et al., 1994, 1995; Schneider et al., 2004b; C. Tsutsumi and M. Kato, unpublished).

Davalliaceae or subfamily Davallioideae has been classified into four to ten genera and about 50 to 130 species, based on morphological characters (Copeland, 1908, 1927, 1940, 1947; Ching, 1940, 1966a, 1966b, 1978; Holttum, 1949, 1955, 1972; Pichi Sermolli, 1977; Kato, 1985; Kramer, 1990; Nooteboom, 1992, 1994). The modern classification was established by Copeland (1927, 1947) who recognized eight genera in the family, i.e. *Araiostegia* Copel. (including *Gymnogrammitis* Griffith), *Davallia* Sm., *Davallodes* Copel., *Humata* Cav., *Leucostegia* C.Presl, *Parasorus* Alderw., *Scyphularia* Fée, and *Trogostolon* Copel., based on the form, cutting, and texture of leaves, and on scales, pubescence, and the form and size of sori. Holttum (1949) classified subfamily Davallioideae (excluding *Rumohra* Raddi) into five genera, i.e. *Araiostegia*, *Davallia* (including *Parasorus*, *Scyphularia*, and *Trogostolon*), *Davallodes*, *Humata*, and *Leucostegia*. Ching (1940) recognized the genus

Gymnogrammitis and classified the subfamily Davallioideae (excluding *Acrophorus* C.Presl) into eight genera, *Davallia*, *Davallodes*, *Humata*, *Gymnogrammitis*, *Leucostegia*, *Parasorus*, *Trogostolon*, and *Scyphularia*. Later Ching (1966b) separated a new genus *Paradavallodes* Ching from *Araiostegia* and *Davallodes*, while the genus was not judged worthy of recognition by many authors (Sen et al., 1972; Kato, 1985; Kramer, 1990; Nooteboom, 1992, 1994). Pichi Sermolli (1977) recognized 10 genera, including *Gymnogrammitis* and *Paradavallodes*. Kato (1985) proposed a classification that Davalliaceae comprises nine genera (*Araiostegia*, *Davallia*, *Davallodes*, *Gymnogrammitis*, *Pachypleuria* C.Presl, which consists of *H. repens* and related species except for *H. ophioglossa* Cav. [type of *Humata*], *Leucostegia*, *Parasorus*, *Scyphularia*, and *Trogostolon*). Kato (1975, 1985) divided *Davallia* into three sections, sect. *Cordisquama* M.Kato, sect. *Davallia*, and sect. *Wibelia* (Bernh.) M.Kato, based mainly on scale morphologies, i.e. pseudopeltate *vs.* peltate bases, and toothed margins *vs.* hairy margins. Kramer (1990) reduced *Humata*, *Parasorus*, *Scyphularia*, and *Trogostolon* into *Davallia* and consequently recognized five genera (*Araiostegia*, *Davallia*, *Davallodes*, *Gymnogrammitis*, and *Leucostegia*). Later Nooteboom (1992, 1994) reduced more than 100 known species into 49 species in four genera, *Davallodes*, *Gymnogrammitis*, *Leucostegia*, and *Davallia* with two sections, sect. *Davallia* and sect. *Scyphularia* (Fée) Noot. *Araiostegia*, *Humata*, *Parasorus*, *Scyphularia*, and *Trogostolon* were synonymized with *Davallia*.

Gymnogrammitis with exindusiate sori had been included in *Araiostegia* (Copeland, 1947) or treated as an independent family Gymnogrammitidaceae (Ching, 1966a). Later *Gymnogrammitis* was treated as a monotypic genus belonging in the Davalliaceae (Sen and Sen, 1971; Pichi Sermolli, 1977; Kato, 1985; Kramer, 1990; Nooteboom, 1992, 1994). A recent molecular analysis revealed that *Gymnogrammitis* has a close relationship with *Selliguea* Bory of Polypodiaceae (Schneider et al., 2002).

Thus, the classifications and suggested relationships of Davalliaceae differ considerably among authors. It is partly because no comprehensive phylogenetic analysis has been performed for the family. The present study investigated the intrafamilial relationships of Davalliaceae by a molecular phylogenetic analysis.

MATERIALS AND METHODS

Plant material

Among the genera that have been referred to Davalliaceae, *Gymnogrammitis* and *Leucostegia* were excluded from the analysis. *Gymnogrammitis* is a member of Polypodiaceae (Schneider et al., 2002), and *Leucostegia* is related to *Hypodematium* Kunze, a non-davallioid genus (C. Tsutsumi and M. Kato, unpublished). *Parasorus*, *Paradavallodes* and *Trogostolon* were not examined because no material was available. The generic concepts adopted here follow Copeland (1947) except for *Davallodes*, which was recognized in Holttum's (1972) sense. Five genera and 38 individuals (representing 36 species and one variety) and two outgroups were examined (Table 1). They include the species that are referred to three sections of *Davallia* sensu Kato (1985). Leaves were personally provided by friends and colleagues or collected in the field and dried with silica gel. Vouchers are deposited in the University of Tokyo Herbarium (TI)

Phylogenetic analyses

DNA was extracted by a modified CTAB method of Doyle and Doyle (1987) or using

DNeasy Mini Kit (Qiagen, Inc.) following the manufacturer's instruction. Five continuous chloroplast regions were analyzed: *atpB* gene, which is useful for fern phylogeny (Wolf, 1997), *rbcL*, *accD*, *atpB-rbcL* spacer and *rbcL-accD* spacer, a combination of which provided highly resolved intrafamilial relationships in *Hymenophyllum* Sm., Hymenophyllaceae (Ebihara et al., 2003). The region of *atpB* and *atpB-rbcL* spacer was amplified using primers CT-*atpB*R1 (5'-ATTGACCCTCCACTTGTAAAG-3') and *rbcL*-TW2pR (Murakami et al., 1999), *rbcL* region by *rbcL*-aF and *rbcL*-cR (Hasebe et al., 1994) or CT-*rbcL*F1 (5'-ACCCAWGTCACCACAAACRGAG-3') and CT-*rbcL*R4 (5'-CTCCACTTACTWGCWTCRCGAA-3'), and the region of *rbcL-accD* spacer and *accD* by *rbcL*-cF (Hasebe et al., 1994) and CT-*accD*R2 (5'-ACACCTTTTAAGAGATTACGTGG-3'; A. Ebihara, Univ. Tokyo, pers. comm.). PCR was performed using a DNA thermal cycler (Perkin-Elmer 9700, Applied Biosystems, Foster, CA) with *Ex Taq* DNA polymerase (TaKaRa Biomedical, Tokyo). Some samples were amplified with Amp direct (Shimadzu, Kyoto), while most others were amplified with the Ex buffer. PCR products were purified with GFX DNA and GEL purification Kit (Amarsham Pharmacia Biotech, Piscataway, NJ) or with ExoSAP-IT (USB corporation, Ohio) following the manufacturer's instruction.

The PCR products were sequenced with the Big Dye Terminator Cycle Sequencing Kit Ver. II or Ver. III (Applied Biosystems) following manufacturer's instructions with the amplification primers and additional internal primers: CT-*atpB*1334R (5'-TTCTTTCYTGYAATGATCCCATTTC-3', modified from Wolf, 1997), CT-*atpB*1163F (5'-ATGGCRGAATACTTYCGAGATTA-3', modified from Wolf, 1997), CT-*atpB*F1 (5'-TTTATGGTCAGATGAATGAACCA-3'), CT-*atpB*R2 (5'-TTTCCAACTCCAGCCCCACCRA-3'), CT-spacerR1 (5'-GGTGTATTATCTYTATTTGATTA-3'), CT-spacerF (5'-ATCTATAGCTACATCTGCAAAA-3'), CT-spacerR2 (5'-AAGAGATTCCCKAGTCAATGTAT-3'), CT-*rbcL*R1 (5'-CACCAGCTTTGAATCCAAMACCTG-3', modified from Wolf, 1997), CT-*rbcL*F2 (5'-AGCCWTTCATGCGTTGGAGAG-3'), *rbcL*-aR (Hasebe et al, 1994), CT-*rbcL*F3 (5'-TGGCACATGCCYGCTCTAACCGA-3'), CT-*rbcL*R3.5 (5'-CGAGCYTGTACSCAAGCWTCTAA-3'), CT-*accD*F2 (5'-ATGAARACATGACYACAAARATGT-3') CT-*accD*R1 (5'-CCTATACCTGTTTGAACAGCRTC-3') (Fig. 1). The dye was removed by ethanol precipitation and samples were run on an ABI PRISM 377 or ABI PRISM 3100 automated sequencer (Applied Biosystems).

Sequences obtained were assembled using Autoassembler (Applied Biosystems). Assembled sequences were manually aligned after alignment by Clustal X (Thompson et al., 1997). In *atpB* and *accD*, the parts of the regions obtained in most species examined were used for the analysis. An ambiguously aligned region in *atpB-rbcL* spacer consisting of mainly poly (G) with some substitutions and a long insertion (492 bp) in *rbcL-accD* spacer seen only in *Oleandra wallichii* (Hook.) C.Presl were excluded from the analysis. Gaps were treated as missing data.

Phylogenetic analyses were performed using each of five combined chloroplast datasets (4933 bp), single chloroplast regions, coding regions, and non-coding regions by PAUP* 4.0b10 (Swofford, 2002). In maximum parsimony (MP) analyses, all characters were equally weighed and heuristic searches were conducted with 1000 random addition replicates involving TBR branch swapping. Bootstrap values were

Table 1: Species used in molecular phylogenetic analysis, sources and GenBank accession numbers.

Genus and species	Source and voucher	GenBank accession no. of *atpB-accD*
Araiostegia		
A. faberiana (C.Chr.) Ching	China; *CT1068*	AB212688
A. hymenophylloides (Blume) Copel.	Mt. Kinabalu, Sabah, Malaysia; *CT1012*	AB212689
A. parvipinnula (Hayata) Copel.	Mt. Ali, Taiwan; *CT1014*	AB212690
A. perdurans (Christ) Copel.	China; *CT1069*	AB212691
A. pulchra (D.Don) Copel.	Sikkim, India; *CT1016*	AB212692
A. yunnanensis (Christ) Copel.	China; *CT1070*	AB212693
Davallodes		
D. borneense (Hook.) Copel.	Poring, Sabah, Malaysia; *ML94*	AB212694
D. burbidgei C.Chr. & Holttum	Mahua, Sabah, Malaysia; *ML100*	AB212695
D. gymnocarpum Copel.	Philippines; *CT1042*	AB212696
Davallia		
D. corniculata T.Moore	Cibodas, Java, Indonesia; *IN30*	AB212697
D. denticulata (Burm.f.) Mett. ex Kuhn	West Sumatra, Indonesia; *CT1019*	AB212698
D. denticulata (Burm.f.) Mett. ex Kuhn	Philippines; *CT1021*	AB212699
D. divaricata Blume	Irian Jaya, Indonesia; *CT1020*	AB212700
D. embolostegia Copel.	Sabah, Malaysia; *ML56*	AB212701
D. epiphylla (G.Forst.) Spreng.	French Polynesia (Tahiti); *CT1022*	AB212702
D. fejeensis Hook.	Fiji; *CT1024*	AB212703
D. formosana Hayata	Taiwan; *CT1025*	AB212704
D. griffithiana Hook.	Taiwan; *CT1026*	AB212705

D. mariesii T.Moore ex Baker	Gunma pref., Japan; *CT1029*	AB212706
D. aff. *mariesii* T.Moore ex Baker	purchased; *CT1018*	AB212707
D. mariesii var. *stenolepis* (Hayata) Hoshiz.	Okinawa pref., Japan; *CT1030*	AB212708
D. petelotii Tard.-Blot & C.Chr.	purchased in Laos; *CT1031*	AB212709
D. plumosa Baker	West Samoa, Samoa; *CT1032*	AB212710
D. pyxidata Cav.	Queensland, Australia; *CT1033*	AB212711
D. solida (G.Forst.) Sw.	New Caledonia; *CT1034*	AB212712
D. tasmani Field	Univ. of Auckland, New Zealand; *CT1035*	AB212713
D. trichomanoides Blume	Malaysia; *CT1036*	AB212714
D. tyermanii T.Moore	purchased; *CT1039*	AB212715
Humata		
H. banksii Alston	French Polynesia (Tahiti); *CT1049*	AB212716
H. melanophlebia Copel.	French Polynesia (Tahiti); *CT1047*	AB212717
H. parvula (Wall. ex Hook. & Grev.) Mett.	Unknown; *CT1048*	AB212718
H. aff. *parvula (Wall. ex Hook. & Grev.) Mett.*	Genting Highland, Malaysia; *CT1055*	*AB212719*
H. polypodioides Brack.	Fiji; *CT1050*	AB212720
H. aff. *polypodioides* Brack.	Vanuatu; *CT1052*	AB212721
H. vestita (Blume) T.Moore	Cibodas, Java, Indonesia; *IN24*	AB212722
Scyphularia		
S. pentaphylla (Blume) Fée	Java, Indonesia; *CT1058*	AB212723
S. pycnocarpa (Brack.) Copel.	Fiji; *CT1060*	AB212724
S. triphylla (Hook.) Fée	Bogor Botanic Garden, Java, Indonesia; *IN113*	AB212725
Arthropteris backleri (Hook.) Mett.	Queensland, Australia; *AU308*	AB212686
Oleandra wallichii (Hook.) C.Presl	Chiang Mai, Thailand; *TH10*	AB212687

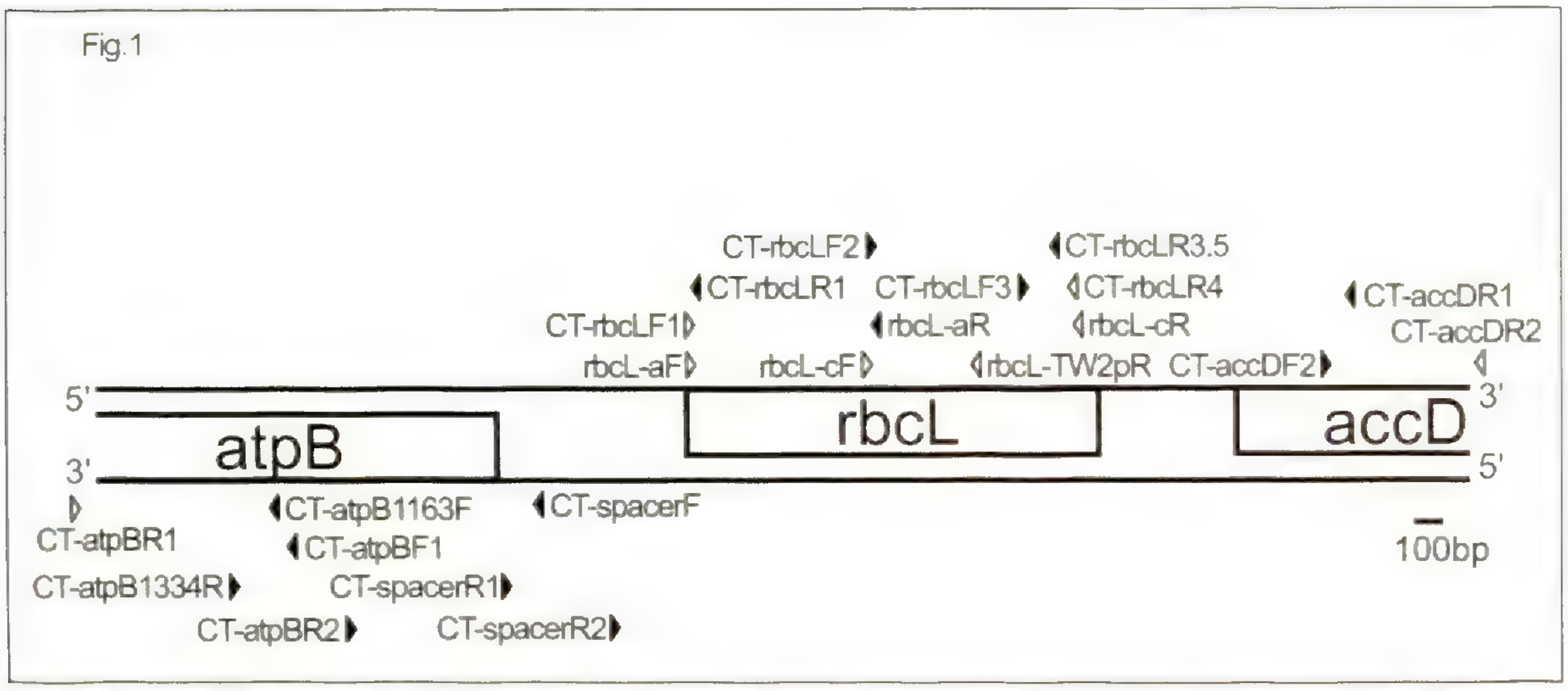

Figure 1. Positions and directions of primers used to amplify and sequence *atpB*, *atpB-rbcL* spacer, *rbcL*, *rbcL-accD* spacer, and *accD*. Open arrowheads indicate external primers and solid arrowheads, internal primers.

calculated with 1000 replicates with 100 random addition replicates for the combined dataset, and with 100 replicates with 10 random addition replicates for the single regions, the coding regions, and the non-coding regions. Bootstrap values for the combined dataset were calculated with 1000 replications by neighbor joining (NJ) method with Kimura-2-parameter model of nucleotide substitutions (Kimura, 1980). In the maximum likelihood (ML) method, Modeltest Ver. 3.5 (Posada and Crandall, 1998) was used to determine the nucleotide substitution model. The GTR + I + G model and gamma rates were selected for our dataset using Akaike informative criterion (AIC). ML analysis was implemented using PAUP 4.0b10 as heuristic searches involving NII branch swapping with 100 random addition sequence replicates. Bayesian inference of phylogeny was performed using MrBayes 3.0 to estimate posteriori supports of clades in ML tree (Huelsenbeck and Ronquist, 2001) with the nucleotide model determined by MrModeltest 2.0 (Nylander, 2004). Bayesian searches were conducted by mcmc with four chains over one million generations, sampling every 100 generations. Two hundred trees obtained before stationary generations were discarded as burn-in trees, and the remaining trees were used in calculating the majority rule consensus tree. *Arthropteris backleri* (Hook.) Mett. and *Oleandra wallichii* were used as outgroups (Hasebe et al., 1994, 1995; C. Tsutsumi and M. Kato, unpublished).

Homogeneity among the different datasets was calculated with the ILD test (Farris et al., 1995; Johnson and Soltis, 1998) as implemented in PAUP. The ILD test was conducted by heuristic search with 100 replicates, using 10 random additions with parsimony-uninformative characters excluded. The ILD test was performed between two of the five datasets, between two coding regions, i.e. *atpB* vs. *rbcL* + *accD*, *rbcL* vs. *atpB* + *accD*, and *atpB* + *rbcL* vs. *accD*, and between the coding region and the non-coding region.

RESULTS

In *accD*, a start codon (ATG) was not found in any species examined, like in other higher leptosporangiate ferns (C. Tsutsumi and M. Kato, unpublished). RNA-editing in transcripts is known in the fern chloroplast genome (Ebihara et al., 2002, Wolf et al., 2004), and in *Adiantum capillus-veneris* L., 90% of RNA-editing is a change from C to

U (Wolf et al., 2004). In our study, all species examined had ACG near a start codon of *accD* gene in the known genome of other ferns. Therefore, the *rbcL-accD* spacer and *accD* were separated in front of the ACG codon.

The non-coding regions had more informative characters (17-19%) than the coding regions (8-10%) (Table 2). All ILD-tests for different partitions tested indicated that *p*-values were higher than 0.05 (the lowest *p*-value was 0.24 between *atpB-rbcL* spacer and *rbcL*) and the datasets were not incongruent.

Deduced phylogenies based on the combined five chloroplast regions (Figs. 2, 3) showed that none of the genera of Davalliaceae examined are monophyletic. *Araiostegia* was divided between two clades (*Araiostegia* clades 1, 2); *Araiostegia* clade 1 included *A. hymenophylloides* (Blume) Copel., *A. pulchra* (D.Don) Copel. and *A. yunnanensis* (Christ) Copel., while *Araiostegia* clade 2 comprised *A. faberiana* (C.Chr.) Ching, *A. parvipinnula* (Hayata) Copel. and *A. perdurans* (Christ) Copel. *Davallodes* was a component of *Araiostegia* clade 1. *Davallia* was divided to three clades (*Davallia* clades 1-3); *Davallia* clade 1 included *D. griffithiana* Hook., *D. mariesii* T.Moore ex Baker, *D. petelotii* Tard.-Blot & C.Chr., *D. trichomanoides* Blume and *D. tyermanii* T.Moore; *Davallia* clade 2 comprised *D. fejeensis* Hook., *D. plumosa* Baker, *D. pyxidata* Cav., *D solida* (G.Forst.) Sw. and *D. tasmani* Field; and *Davallia* clade 3 consisted of *D. denticulata* (Burm.f.) Mett. ex Kuhn, *D. divaricata* Blume, *D. embolostegia* Copel., *D. epiphylla* (G.Forst.) Spreng., and *D. formosana* Hayata. All examined species of *Humata* and *Davallia corniculata* T.Moore formed a monophyletic clade. *Scyphularia* was paraphyletic; *S. pycnocarpa* (Brack.) Copel. and *S. pentaphylla* (Blume) Fée were sister to *Davallia* clade 2 and together sister to *S. triphylla* (Hook.) Fée.

Furthermore, the trees showed that the clade consisting of *Araiostegia* clade 1 and *Davallodes* was the most basal in Davalliaceae. The next diverging group was *Davallia* clade 3. *Araiostegia* clade 2 was sister to the remaining species in the ML tree (Fig. 3), although the relationships among *Araiostegia* clade 2, *Humata*, and *Davallia* clade 1 + *Davallia* clade 2 + *Scyphularia* remained unsolved in the strict consensus tree (Fig. 2). *Davallia* clade 1 and *Davallia* clade 2, along with *Scyphularia*, formed a monophyletic clade with moderately high credibility.

The strict consensus trees based on each of the five datasets were constructed by MP analysis (Table 2; trees not shown). Although the *accD* and *rbcL-accD* spacer trees included polytomies, their topologies were consistent in general with those of the combined trees (Figs. 2, 3). The other genes and spacer had some parts of branches inconsistent with those of the combined trees. *Araiostegia* clade 1 was paraphyletic in the *atpB* and *atpB-rbcL* spacer trees. In the *accD* tree, clade *Humata* formed a monophyletic clade along with *Davallia* clade 1; on the other hand, clade *Humata* formed a monophyletic clade along with *Araiostegia* clade 2 in the *atpB* tree. Supports for those topologies that were different from those of the combined trees were weak (<60%).

In the sequences obtained (4933 bp), there was no substitution between *Davallia mariesii* and *D. mariesii* var. *stenolepsis* (Hayata) Hoshiz., between *D. solida* and *D. fejeensis*, and between *Humata polypodioides* Brack. and *H.* aff. *polypodioides*. There were only one or two substitutions between *Davallia denticulata* (Sumatra) and *D. denticulata* (Philippines), between *D. plumosa* and *D. solida* (*D. fejeensis*), between *Humata banksii* Alston and *H. melanophlebia* Copel., and between *Scyphularia pentaphylla* and *S. pycnocarpa*.

Table 2: Results of maximum parsimony analyses of different datasets.

	Mps	L	IN/CH	Ratio	CI	HI	RI	RC
atpB	1	247	120/1393	8.61%	0.7310	0.2690	0.8861	0.7211
rbcL	592	339	136/1428	9.52%	0.5742	0.4258	0.7904	0.5362
accD	248	153	67/811	8.26%	0.6961	0.3039	0.8703	0.6940
atpB-rbcL spacer	12	296	129/694	18.59%	0.7488	0.2512	0.8753	0.7245
rbcL-accD spacer	339	276	107/607	17.63%	0.6750	0.3250	0.8556	0.6541
coding region	12	747	323/3632	8.89%	0.6387	0.3613	0.8332	0.6168
non-coding region	46	575	236/1301	18.14%	0.7069	0.2931	0.8615	0.6832
all combined datasets	4	1324	559/4933	11.33%	0.6667	0.3333	0.8442	0.6434

Mps, number of most parsimonious trees; L, tree length; IN/CH, number of parsimony informative characters per total number of included characters; Ratio, ratio of number of informative characters to total number of characters; CI, consistency index excluding uninformative characters; HI, homoplasy index excluding uninformative characters; RI, retention index; RC, rescaled consistency index.

DISCUSSION

Phylogenetic relationships based on different genes and spacers

The trees of the three coding regions, *atpB*, *rbcL*, and *accD*, and two non-coding regions, *atpB-rbcL* spacer and *rbcL-accD* spacer, each include polytomies in some different branches, and parts of the inferred relationships are not highly resolved (data not shown). In contrast, the tree obtained by analyses of the combined dataset is highly resolved and comprises mostly robustly supported branches (Figs. 2, 3). The non-coding regions have twice as many informative characters as the coding regions (Table 2). The non-coding regions are useful for intrafamilial phylogenetic analysis, although *rbcL-accD* spacer is too variable to align objectively to infer the interfamilial relationships of higher leptosporangiate ferns (C. Tsutsumi and M. Kato, unpublished).

Phylogeny and systematics of Davalliaceae

The molecular intrafamilial phylogenetic relationships of Davalliaceae differ considerably from previous classifications based on comparative morphology (Copeland, 1947; Holttum, 1949; Ching, 1940, 1978; Pichi Sermolli, 1977; Kato, 1985; Kramer, 1990; Nooteboom, 1992, 1994). The genus *Humata* was typified by *H. ophioglossa*, which, like *H. heterophylla* (Sm.) Desv., is characterized by the dimorphic leaf, i.e. simple sterile leaf and pinnatifid fertile leaf. In most classifications, *Humata* included these two species, *H. repens* (L.f.) Diels, and related species (Copeland, 1927, 1940, 1947; Holttum, 1955; Pichi Sermolli, 1977; Ching, 1978), although the genus was reduced in *Davallia* sensu lato (Kramer, 1990; Nooteboom, 1994). Copeland (1927) characterized *Humata* as usually having dimorphic and coriaceous leaves, medium-sized sori, and firm or coriaceous and basifixed indusia. Later, Copeland (1940, 1947) pointed that some diagnostic characters are inconsistent and Holttum (1955) suggested that *Humata* is a heterogeneous assemblage. Kato (1985) transferred *H. ophioglossa* (type of *Humata*) to *Davallia* sect. *Wibelia* and recognized the genus *Pachypleuria* for *H. repens* and related species based on the scale characters, such as peltate base, toothed margin, and smooth surface. The present study did not examine *H. ophioglossa* because material was not available and further study is needed to examine the relationship of *H. ophioglossa* and *H. heterophylla* to settle the systematics and nomenclature of the species. *D. corniculata* has been referred to the genus *Davallia* by the medium-sized, compound leaf, and sometimes cup-shaped indusia (Holttum, 1955; Kato, 1985). The molecular data indicate that *D. corniculata* is a member of the *Humata* clade. It is consistent with morphological similarities, i.e. coriaceous and slightly dimorphic leaf, often shell-shaped indusia, and white waxy rhizome.

The genus *Davallodes*, based on *D. hirsutum* (J.Sm. ex C.Presl) Copel. (Copeland, 1927), comprises nine species (Holttum, 1972). It is characterized by the leaves being attenuate downward and bearing multicellular articulate hairs, the scales peltate (rarely pseudopeltate) and acicular (rarely broad), and the pinnules catadromous (Holttum, 1972; Kato, 1985). The delimitation of the genus and *Araiostegia* remains unsettled. Holttum (1972) removed *D. membranulosum* (Wall. ex Hook.) Copel. to *Araiostegia*, while Ching (1966b) established *Paradavallodes* comprising *Araiostegia multidendata* (Hook.) Copel., *D. membranulosum*, and two more Chinese species. Our trees constructed by long sequences (4933 bp) could not support the view that the species of *Davallodes* examined form a monophyletic group.

Araiostegia is separated into two remote clades, which can be distinguished only by

Fig. 2

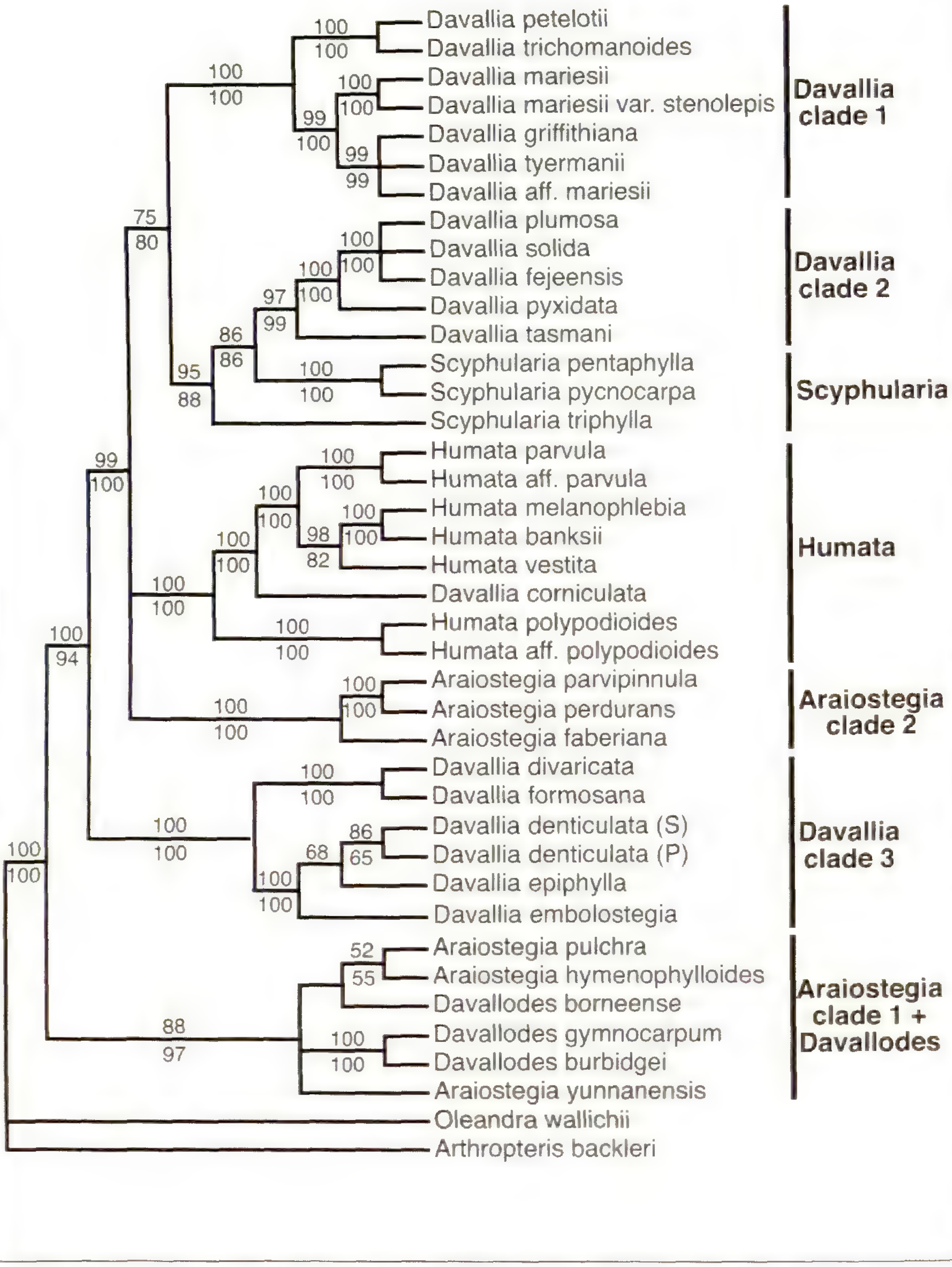

Figure 2. Strict consensus tree of four trees of Davalliaceae obtained by MP method based on combined *atpB*, *rbcL*, *accD atpB-rbcL* spacer, and *rbcL-accD* spacer sequences (4933 bp). Results of MP analysis are shown in Table 2. Figures above branches indicate bootstrap values (> 50%) by MP method and figures below branches, those by NJ method. Data of species are shown in Table 1. *Oleandra wallichii* and *Arthropteris backleri* were used for outgroups (Hasebe et al., 1994, 1995; C. Tsutsumi and M. Kato, unpublished). P, Philippines; S, Sumatra.

Fig. 3

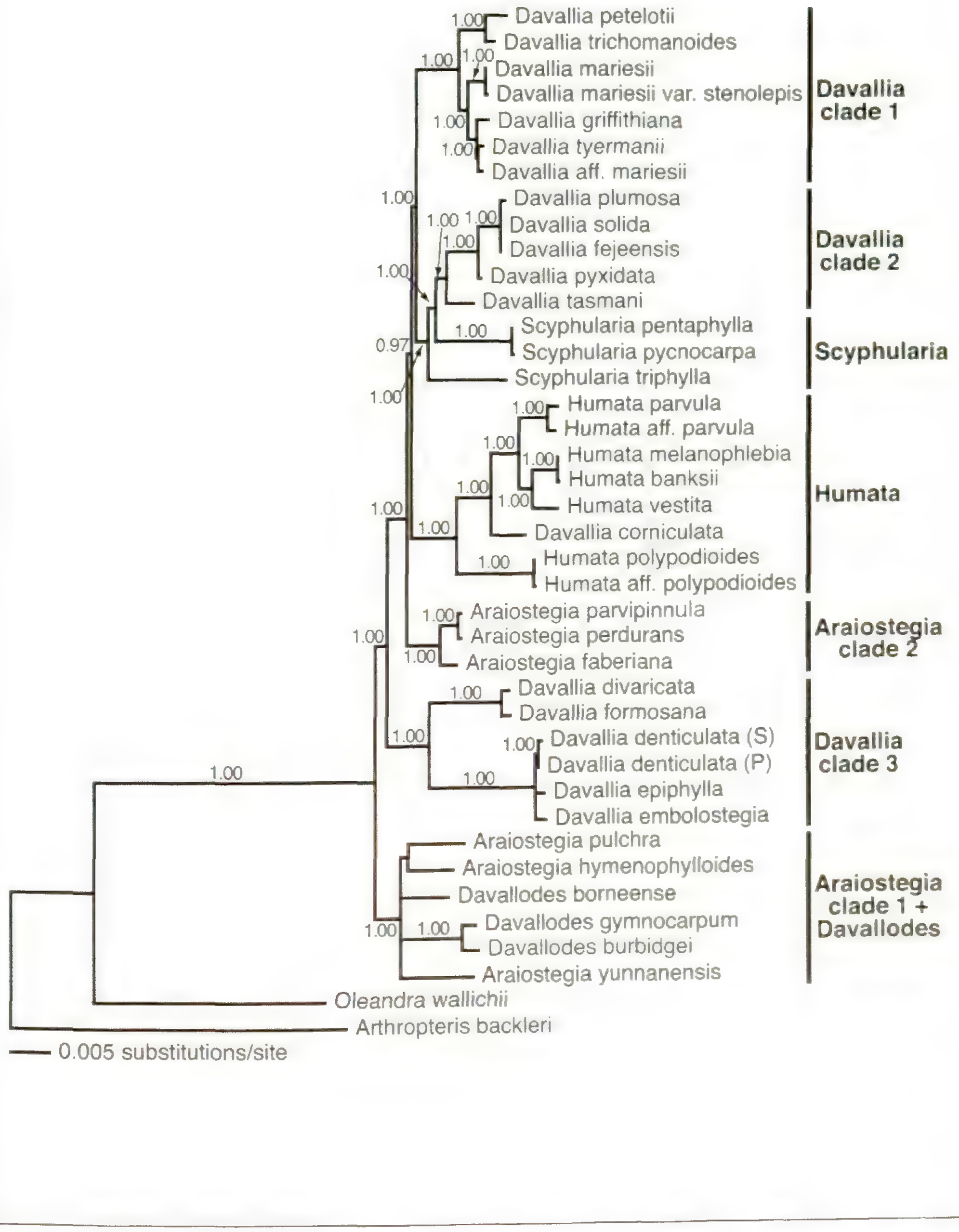

Figure 3. ML tree (-ln = 14965.32630) of Davalliaceae based on combined *atpB*, *rbcL*, *accD atpB-rbcL* spacer, and *rbcL-accD* spacer sequences (4933 bp). Figures indicate posterior probabilities (> 0.9) calculated by bayesian analysis. P. Philippines: S. Sumatra.

the presence (*Araiostegia* clade 1) or absence (*Araiostegia* clade 2) of pinna and pinnule stalks. *Araiostegia* clade 1 + *Davallodes* diverges the most basally and is a morphologically heterogeneous group, while *Araiostegia* clade 2 is nested within the rest of Davalliaceae. *Araiostegia* clade 1 + *Davallodes* has stalked pinnae in common, while there are variations in the scales (peltate or pseudopeltate), leaf form (deltoid, lanceolate, or oblanceolate), hairs (multicellular or glabrous), and indusia (reniform, cup-shaped or shell-shaped). It is noted that continental Asian species are separated in the two subclades; *A. pulchra* and *A. yunnanensis*, along with Malesian *A. hymenophylloides* as well as *Davallodes*, form clade *Araiostegia* 1 + *Davallodes*, and all the species of *Araiostegia* clade 2 are continental Asian.

By such specialized characters as simple or imparipinnate leaves and acicular scales, *Scyphularia* is segregated from the other genera (Copeland, 1947; Kato, 1985) or recognized as a section of *Davallia* sensu lato (Nooteboom, 1994). Simple leaves are rarely seen in *Humata* and *Parasorus*, and no other species has imparipinnate leaves. Eight species assigned to the genus are distributed in Malesia and Pacific islands. In spite of the shared specialized morphologies, the results show that the genus is paraphyletic. Furthermore, it is closely related to clade *Davallia* 2 comprising *D. solida*, *D. pyxidata* and other species, as *Scyphularia* and *Davallia* clade 2 share hairy scales and elongate sori (Kato, 1985). From this result it is inappropriate to treat *Scyphularia* as an independent genus or as a section of *Davallia*.

The phylogenetic tree shows that *Davallia* is not a monophyletic group. It is not congruent with any current classifications irrespective of whether the genus is treated in a narrow or broad sense (Copeland, 1947; Holttum, 1947, 1955; Pichi Sermolli, 1977; Ching, 1978; Kato, 1985; Kramer, 1990; Nooteboom, 1992, 1994). Three clades of *Davallia* coincide in large measure with three sections of *Davallia* (Kato, 1985); *Davallia* clade 1 corresponds to sect. *Wibelia*, *Davallia* clade 2 to sect. *Davallia*, and *Davallia* clade 3 to sect. *Cordisquama*. Among the clades, *Davallia* clade 2 + *Scyphularia* is sister to *Davallia* clade 1. The two clades are distinguished by the scales: the scales of *Davallia* clade 2 + *Scyphularia* are hairy at the margin, and those of *Davallia* clade 1 are toothed. *Davallia* clade 3 diverges between the basal clade (*Araiostegia* clade 1 + *Davallodes*) and the rest of the family. The two basal clades include species (e.g. *Davallia divaricata*, *Araiostegia* species) with pseudopeltate scales, which were speculated to be primitive compared with peltate scales (Kato, 1975). This speculated trend of scale evolution is associated with that of soral-position evolution (Kato, 1975). Sori are situated at angled points of veins in *Araiostegia* except for *A. yunnanensis*, *Davallodes*, *Davallia divaricata* and *D. formosana*. The sori of the other species are positioned at vein bifurcations.

D. denticulata and *D. epiphylla* are included in *Davallia* clade 3. These species have peltate, toothed scales similar to those of sect. *Wibelia*, while the rest of *Davallia* clade 3 (*D. divaricata*, *D. embolostegia*, and *D. formosana*) have pseudopeltate scales (Kato, 1985). Disagreement between the molecular phylogeny and the aforementioned character association of scales and soral positions may be given alternative explanations. The scales and soral positions similar to those of *Davallia* clade 1 or sect. *Wibelia* may be independently derived in *Davallia* clade 3. Or *D. denticulata* and *D. epiphylla* may be products of hybridization involving species close to *D. embolostegia* as maternal parents and unknown species assignable to *Davallia* clade 1 as paternal parents. Further studies using nuclear genomic sequences may reveal their relationships.

Our results also raise interesting issues to be solved. *Davallia fejeensis* has the same sequences as *D. solida*, although *D. fejeensis* is differentiated from *D. solida* or regarded as a variety of it, based on some morphological characters. *D. fejeensis* may be a mutant with finely dissected leaves, and consequently having sori that are frequently single (several in *D. solida*) in single segments, and veins in sterile ultimate lobes frequently simple (pinnate in *D. solida*).

As noted above, none of the genera that have been recognized in previous classifications (see Introduction) are monophyletic, but rather polyphyletic or paraphyletic. This result requires a considerable taxonomic revision. If Davalliaceae were to be treated as a single large genus (*Davallia*), the genus should be classified at infrageneric rank. If the family were to be divided into three genera, based on clades *Araiostegia* 1 + *Davallodes*, *Davallia* clade 3, and the rest of the clade, then substantial taxonomic revision would need to reflect respectively the genus *Davallodes* (including *Araiostegia*), a new genus, and the genus *Davallia* (including *Humata*, *Scyphularia* and others) . Although this classification appears similar to that of Nooteboom (1992, 1994), the generic concept and infrageneric classification of *Davallia* and *Davallodes* differ considerably. If the family were to be divided into many smaller genera (e.g. *Humata*), different substantial revisions would be needed. It is not easy to define the genera or infrageneric taxa in any of the three cases. It is premature at present to propose a new generic classification of Davalliaceae, along with appropriate definitions of infrafamilial taxa, and a revision should be made only after comprehensive molecular phylogenetic analysis and taxonomic study.

Future perspective for research of epiphyte evolution

Davalliaceae, like polygrammoid ferns (Polypodiaceae + Grammitidaceae), Vittariaceae, part of Hymenophyllaceae and part of Aspleniaceae, are generally epiphytic. The mostly obligate epiphytic families Davalliaceae and polygrammoid ferns form a clade (Hasebe et al., 1995; Schneider et al., 2004b; C. Tsutsumi and M. Kato, unpublished), suggesting that the epiphytic life form arose in the common ancestor of the families. Both groups of families may be sister to a group of *Arthropteris beckleri*, *Oleandra pistillaris* (Sw.) C.Chr. and *Tectaria devexa* (Kunze ex Mett.) Copel., or *O. pistillaris*; the true sister to the families remains uncertain (Hasebe et al., 1995). Phylogenetic research is needed to clarify the sister group of Davalliaceae and polygrammoid ferns in order to investigate the epiphyte evolution of the families. Intrafamilial relationships in each of the families are also useful to infer the epiphyte evolution in the families. In their molecular phylogenetic analysis Schneider et al. (2004a) showed that the basalmost genera in polygrammoid ferns are *Anarthropteris lanceolata* (Hook.f.) Pic.Serm., *Dictymia brownii* (Wikstr.) Copel., and *Loxogramme* (Blume) C.Presl. The present results indicate that *Araiostegia* clade 1 ~ *Davallodes* diverged first in Davalliaceae and *Davallia* clade 3 diverged secondly. Taking those interfamilial and intrafamilial relationships into account, further comparison among life forms of the families and related ferns should be made to infer the evolutionary pathway in which obligate epiphytes were derived from (an) ancestral life form(s) (secondary hemiepiphyte, climber, terrestrial) and how often obligate epiphytes appeared in Davalliaceae, polygrammoid ferns and other epiphytic families.

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DEVELOPMENT OF GAMETOPHYTES FROM GEMMAE OF KILLARNEY FERN (*TRICHOMANES SPECIOSUM* WILLD., HYMENOPHYLLACEAE, PTERIDOPHYTA)

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ABSTRACT

Trichomanes speciosum Willd. (Hymenophyllaceae) is one of the rarest species in the British Isles. One aim of the research programme of which this study formed a part was to understand the requirements for, or tolerance of, extremely deep shade by *T. speciosum* gametophytes. A specific aim was to determine the extent to which macro- and micro-morphological features, in particular reproduction via gemmae, might contribute to the success of this species in deep shade habitats. Another specific aim was to understand how gametophyte growth is affected by different light and temperature conditions.

Gemmae are highly variable in cell number and shape, but typically spindle-shaped or bar-shaped. Once detached, there is no set pattern of growth but photosynthetic cells are typically formed before rhizoids. The highest numbers of photosynthetic cells were produced by gemmae grown in the lowest light level employed in the study: 5µmolm^{-2}s^{-1}, PAR. Most gemmae proved unable to grow in 60 or 90µmolm^{-2}s^{-1}. Gemmae grown at 24°C generated the greatest number of photosynthetic cells and rhizoids in the temperature tested; those grown at 28°C produced the fewest in both light levels tested (5 and 30µmolm^{-2}s^{-1} PAR). Of the conditions tested, PAR of 5µmolm^{-2}s^{-1} and a temperature of 24°C generated optimum gametophyte growth from gemmae cultured on the media used. This is significantly higher than the ambient light levels and temperatures found for most of the time in British field sites, and in line with predictions for a sub-tropical species on the edge of its range. Implications for site and climate perturbation are discussed.

INTRODUCTION

Killarney Fern, or Bristle Fern, (*Trichomanes speciosum* Willd.), is a filmy fern in the Hymenophyllaceae. This fern has been described as one of the rarest in the British flora and was also listed as one of Britain's most vulnerable species in the British Red Data Book (Perring & Farrell, 1983; Ratcliffe *et al.*, 1993). The rarity of the sporophyte of species in Britain has been caused not only by climatic factors that limit its distribution and dispersal (Rumsey *et al.*, 1999), but also through removal by collectors. In the early nineteenth century sporophytes occurred in local profusion, subsequently being reduced considerably by the predation of gardeners, dealers and tourists. Disturbance to microhabitats through visitation still arguably poses threats to the survival of

sporophytes (Rumsey *et al.*, 1998). The plant is protected under the Wildlife and Countryside Act, 1981 in Great Britain and under the Flora Protection Order, 1987 and the Wildlife (NI) Order, 1985 in Ireland (Jermy and Camus, 1993).

It has recently become clear that although the sporophyte is extremely rare and vulnerable in Europe, colonies of gametophytes are sufficiently genetically diverse, numerous and widespread to indicate that "the species is [not] threatened with extinction" (Rumsey *et al.*, 1999; 2005). The significant difference between the generations that accounts for this is their ability to reproduce. The sporophytes are rarely fertile in Britain. Ratcliffe *et al.* (1993) reported that *T. speciosum* sporophyte colonies in Britain do not produce fertile fronds every year, even when growing in what seemed to be favourable habitats. They found only 1 out of 13 British colonies and 4 out of 30 Irish colonies to be fertile at any time. When the (green) spores are produced, they have limited viability and germinate and grow very slowly (Page, 1982; Yoroi, 1972). Gametophytes of this species, on the other hand, are invariably found in a reproductive state (Rumsey, Raine & Sheffield, 1992). The reproduction in question is asexual (sexual organs are very rarely produced) but as genetic diversity between colonies is high (Rumsey *et al.*, 1999), vegetative propagation prevents genetic erosion and can ensure survival of the species.

Most ferns produce gametophytes which are flat, green, cordate and short-lived. Those of *Trichomanes* are branched, filamentous and perennial, ultimately forming extensive mats. The filaments can produce asexual propagules called gemmae. These structures detach readily and may be dispersed well beyond the range of the parent plant. The aim of this study was to find out how they 'germinate' once detached, and to identify conditions conducive to successful growth.

Gametophytes typically occur in habitats subject to mean levels of photosynthetically active radiation (PAR) below 1$\mu molm^{-2}s^{-1}$ and are restricted to sunless, sheltered aspects of sites in Britain (Rumsey, 1994 & Rumsey *et al.*, 1998). However, sporophytes grow in higher PAR in the Azores than they do in Britain and this may also hold for gametophytes (Rumsey, pers. comm.). So one important question we sought to answer was whether British gametophytes are capable of growth in higher light levels than they usually experience.

Raine and Sheffield (1997) observed that gemmae cultured in aseptic medium grew well in PAR of 2 and of 6$\mu molm^{-2}\ s^{-1}$, but were bleached, with swollen cells in a "PAR of >10$\mu molm^{-2}s^{-1}$". However, these authors provided no indication of how far their PAR was in excess of 10$\mu molm^{-2}s^{-1}$ and no previous or subsequent work has quantified the PAR requirement or tolerances of gametophytes.

The microsites occupied by gametophytes do not experience the same fluctuations in humidity as the external environment (RH is typically above 90%), and the same is true for temperature. The annual means of air temperature at two microsites regularly monitored were 7.6°C and 8.4°C. The minimum temperatures were 1.6°C and 1.4°C and the maximum temperatures recorded were 12.7°C and 15°C (Rumsey, 1994). External temperatures rose to at least 27°C in the locality during the period of study. The species is thermophilous, however, and Raine and Sheffield (1997) reported that gemmae in culture produced greater biomass when kept at 20°C than at 12°C, as might be expected for a predominantly tropical species at the edge of its range in Britain. Another important question addressed by our study was therefore whether British gametophytes are capable of even better growth at temperatures in excess of 20°C.

Raine and Sheffield (1997) established *T. speciosum* gametophyte cultures by using gemmae and a limited range of defined media including Moore's (1903) and Hoagland's (Reuter, 1953), at full and one-tenth strength, with and without 2% sucrose and solidified with 0.8% agar. They reported that gemmae germinated and grew on all the media tested, but that the most rapid growth occurred on one-tenth strength Hoagland's with sucrose. The latter defined medium was therefore chosen as the basal medium for gemma cultures in this study to determine the effects of environmental conditions of light and temperature on gametophyte growth.

MATERIALS AND METHODS

Specimens were collected (under licence) from a woodland site near Hebden Bridge, Yorkshire, England (SD980 262). Samples were placed on a sterilized sand surface overlaid with Levington M2 Compost, and dampened with distilled water. Glass crystallising dishes were used as compost culture vessels and were placed in an incubator at 20°C±2°C. Light was supplied by fluorescent daylight tubes and the containers of plants were covered with filter film (Lee filters No. 211) to give PAR of 5$\mu molm^{-2}s^{-1}$ in a 12 h light and 12 h dark cycle.

Gametophytes obtained from the same site were also maintained in cultivation on defined medium in aseptic conditions. These plants were subcultured in 9cm diameter petri dishes on agar following the method described in Raine and Sheffield (1997): one-tenth strength Hoagland's medium with 2% (w/v) sucrose (BDH) was the basal medium, adjusted to pH 5.9 and solidified with 0.8% (w/v) bacteriological agar (Oxoid No.1). The plants were maintained in the same conditions as the plants on compost cultures.

Light and temperature experiments.

The experiments employed the same aseptic cultures and media as used for long term cultivation. Inside a laminar flow unit, gemmae were shaken from agar cultures on to the surface such that each 9cm petri dish contained at least 10 gemmae. The dishes were sealed with laboratory film (Nescofilm), labelled and incubated in a 12h light and 12h dark cycle in which illumination was provided by fluorescent daylight tubes. Different levels of PAR at the level of the dishes were generated by covering the dishes with filter film (Lee filters: No. 209, 210, 211). The gemmae consisted of different numbers of cells when detached, so the cells of each gemma in each plate were counted and the plate lid was demarcated to show the area occupied by each gemma such that it could be relocated. Growth was monitored using a steromicroscope and the number of photosynthetic cells per original gemma cell and the number of rhizoids per original gemma cell recorded.

Light experiment I.

This tested the null hypothesis that four levels of PAR ranging from 5-90 mol m^{-2} s^{-1} do not differ in their effects on gametophyte growth, as measured by production of photosynthetic cells and rhizoids after gemmae have been cultured for 70 days. Dishes were placed in an incubator at 20°C±2°C: PAR values at the level of the dishes were 5, 30, 60 and 90$\mu molm^{-2}s^{-1}$. Three dishes per treatment with at least 10 gemmae in each plate were used as replicates. Cells were counted for each gemma every two weeks for 70 days.

Light experiment II.
The null hypothesis tested was that four levels of PAR ranging from 5-30μmolm^{-2}s^{-1} do not differ in their effects on gametophyte growth, as measured by production of photosynthetic cells and rhizoids after gemmae have been cultured for 120 days. This was set up in the same manner as light experiment I using PAR of 5, 10, 20 and 30μmolm^{-2}s^{-1}. Five dishes per treatment with at least 6 gemmae in each plate were recorded. Cells were counted on each gemma every two weeks for 70 days and then at 90 and 120 days.

Temperature experiment I.
The null hypothesis tested was that temperatures ranging from 20°C to 28°C do not differ in their effects on gametophyte growth after gemmae have been cultured in PAR of 5μmolm^{-2}s^{-1} for 120 days. Incubators were set up at 20°C, 24°C and 28°C and the experimental dishes covered with filter film (Lee filters No. 211) to give PAR of 5μmolm^{-2}s^{-1}. Five experimental dishes per treatment with at least 6 gemmae in each plate were recorded, as in light experiment II.

Temperature experiment II.
The null hypothesis tested was that temperatures ranging from 20°C to 28°C do not differ in their effects on gametophyte growth after gemmae have been cultured in PAR of 30μmolm^{-2}s^{-1} for 120 days. Incubators were set up at 20°C, 24°C and 28°C and the dishes covered with filter film (Lee filters No. 209) to give PAR of 30μmolm^{-2}s^{-1}. Four dishes per treatment with at least 6 gemmae in each plate were recorded, as in light experiment II.

Statistical analysis.
Data were analysed using one-way analysis of variance. The least significant difference (LSD) test was used to detect significant differences between the means from different treatments. For light experiments and temperature experiment I, the mean number of photosynthetic cells per original gemma cell and the mean number of rhizoids per original gemma cell of each treatment were calculated from 30 gemmae. For temperature experiment II, the mean number of photosynthetic cells per original gemma cell and the mean number of rhizoids per original gemma cell of each treatment were calculated from 24 gemmae.

A two-way analysis of variance (Simple Factorial) was used to determine significant differences between mean number of cells per original gemma cell from 30 gemmae cultured in PAR of 5μmolm^{-2}s^{-1} at each of three different temperatures (20°C, 24°C, 28°C) (obtained from temperature experiment I), and of 24 gemmae cultured in PAR of 30μmolm^{-2}s^{-1} at the same temperature (obtained from temperature experiment II), when gemmae were cultured for 120 days.

Microscopy.
Cultures were examined and photographed using a Leica wild stereo microscope and a Cambridge S200 SEM fitted with a Hexland Cryotrans CT1000 chamber (see Sheffield & Farrar, 1988).

RESULTS

Gametophyte and gemma morphology.
Trichomanes speciosum gametophytes are branched filaments, forming mats that are

bright green. No differences of overall mat structure, cellular orientation or content were detected between field-collected specimens and specimens cultured on agar or on potting compost. Gemmae were found on all specimens, including cultures grown from gemmae for only 8 months. They consisted of 1-20 cells and were typically spindle-shaped; some were bar-shaped (Fig 1 a & b). Some spindle-shaped gemmae had two end cells smaller than the other cells. Some gemmae had 3 or 4 arms, referred to as "branched gemmae" (Fig. 1 c & d).

'Germination' of gemmae was invariably slow, and cell division occurred in cells at both ends of the gemmae or occasionally in central cells. The initial stages of growth in

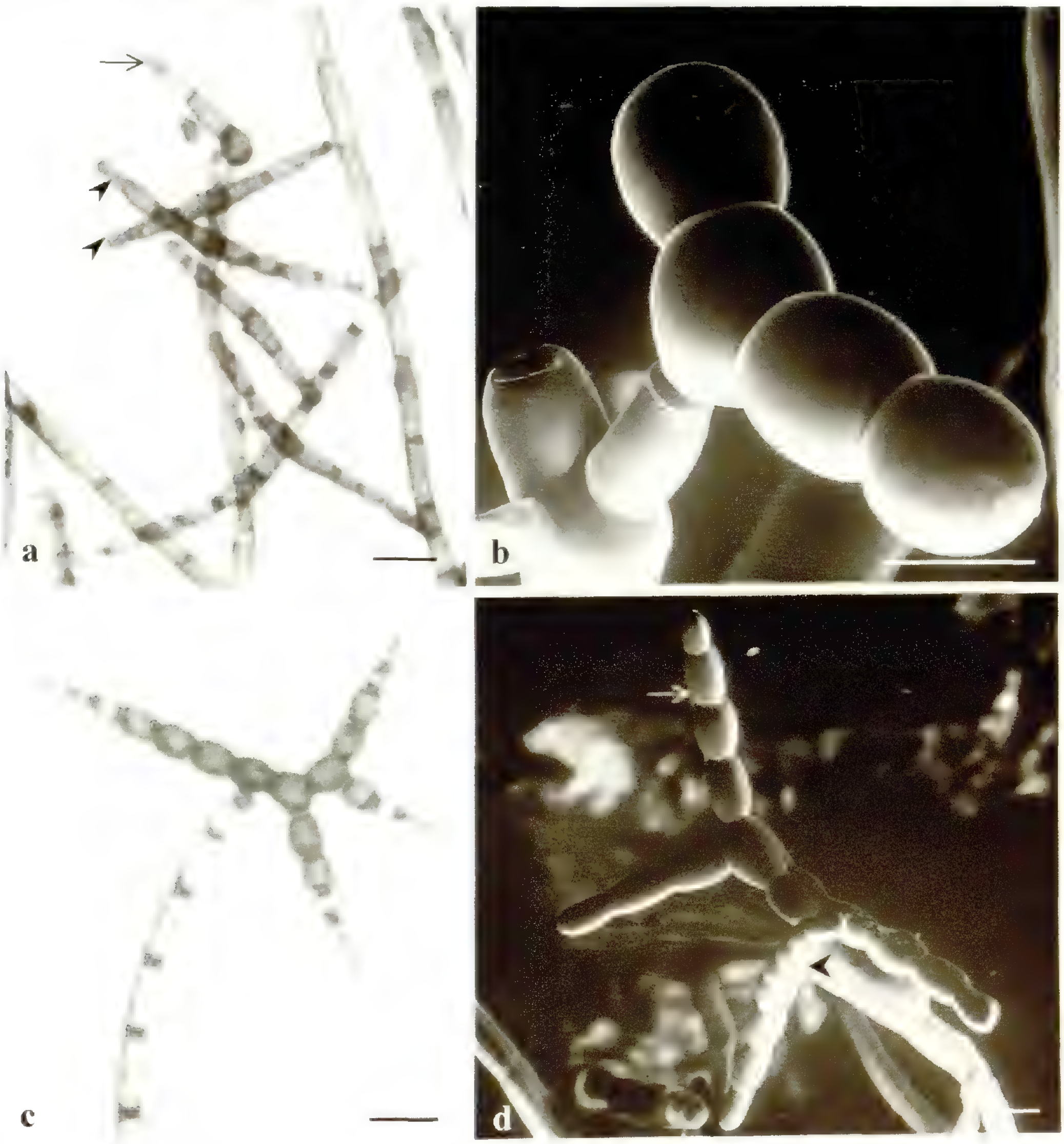

Figure 1. Light and scanning electron micrographs of *T. speciosum* gametophytes showing gemma features (a) Filaments bearing typical spindle-shaped gemmae (arrowheads) and a bar-shaped gemma (arrow) (Bar = 100 μm). (b) A fully developed spindle-shaped gemma has almost detached from the gemmifer and one arm is longer than other (Bar = 50 μm). (c) A branched gemma with 4 arms (Bar = 100 μm). (d) A branched gemma with 4 arms (arrow) with a typical spindle-shaped gemma below (arrowhead) (Bar = 100 μm).

all levels of PAR were similar. Most gemmae produced photosynthetic cells initially but some produced rhizoids first. Growth from the healthiest gemmae then took the form of branched filaments which generated both horizontal and erect branches by the time they had been cultured for 70 days. Rhizoids were positively geotropic and many were able to grow into the medium and anchor the gametophytes. More photosynthetic cells were produced than rhizoids in all gemmae that grew.

Light experiment I.

Most gemmae grown in PAR of 5 and 30µmolm^{-2}s^{-1} had produced both photosynthetic cells and rhizoids after they had been cultured for 70 days (see Fig. 2a). Very few gemmae grown in the higher PAR levels of 60 and 90µmolm^{-2}s^{-1} produced any new cells. Some cells of all gemmae in these conditions, including both original gemma cells and new photosynthetic cells, became brown during culture between 42 and 70 days (see Fig. 2b). After 70 days in culture, gemmae grown in PAR of 5 and 30µmolm^{-2}s^{-1}, had produced ca. 1 photosynthetic cell and slightly less than 1 rhizoid per original gemma cell. Gemmae which did grow in the higher light levels had a slightly higher

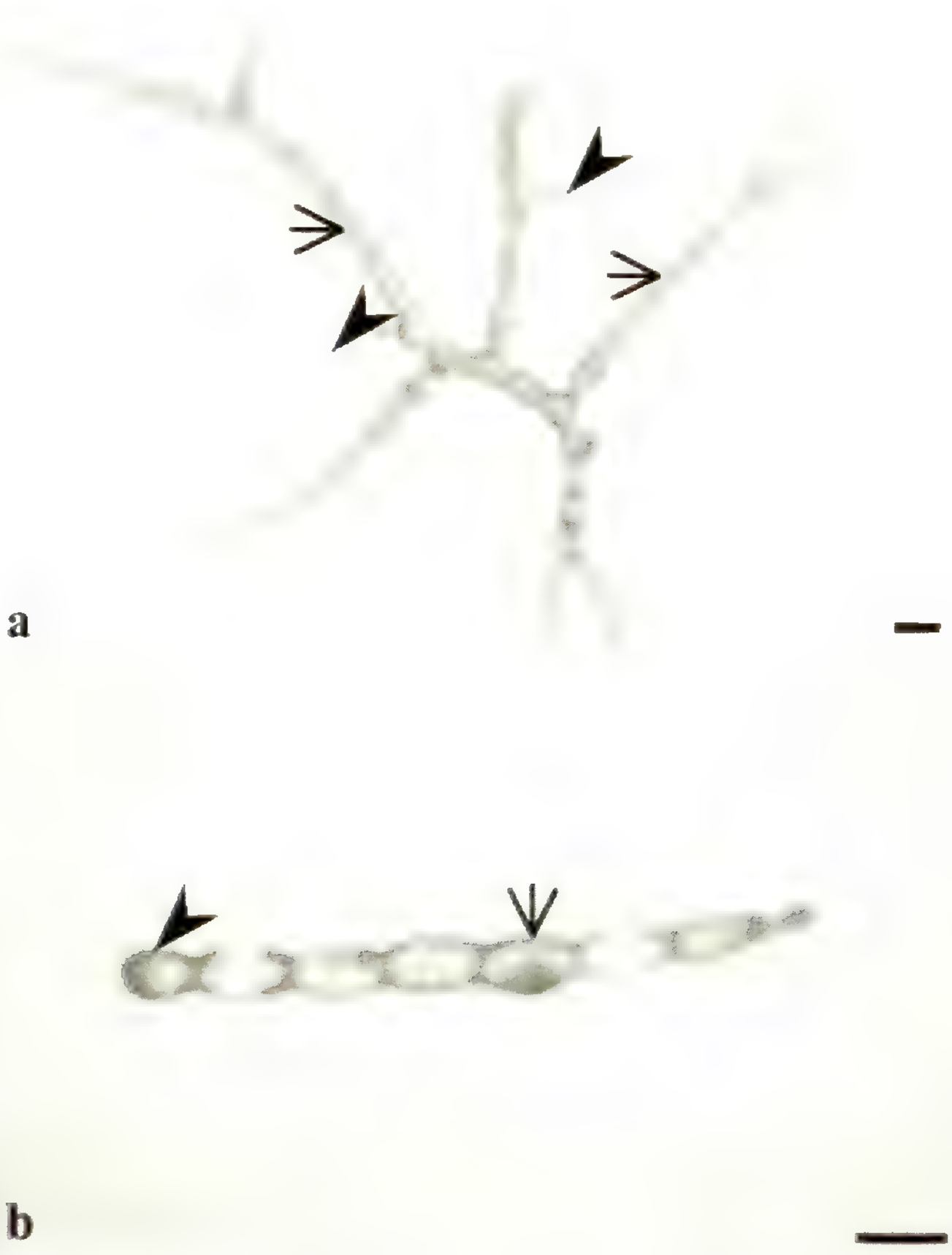

Figure 2. *T. speciosum* gemmae after 70 days in culture at 20C in PAR of 5 and 60µmolm^{-2}s^{-1}. (a) A gemma (9 original cells), typical of those cultured in PAR of 5µmolm^{-2}s^{-1}, which had produced many photosynthetic cells (arrows) and rhizoids (arrowheads). (b) A gemma (6 original cells), typical of those cultured in PAR of 60µmolm^{-2}s^{-1}, some original gemma cells (e.g. arrow) and new photosynthetic cells (e.g. arrowhead) had become brown. (Bars = 100 µm)

proportion of rhizoids to photosynthetic cells but far lower numbers of each than gemmae in lower light levels.

Photosynthetic cell production.

A few gemmae had divided to produce photosynthetic cells when gemmae had been cultured for only 14 days but others delayed production in all levels of PAR tested. By 42 days of culture, gemmae grown in 5 and 30μmolm^{-2}s^{-1} had generated a significantly greater number of photosynthetic cells than gemmae grown in higher PAR levels ($P<0.05$). The mean numbers of photosynthetic cells increased (from ca. 0.34 to ca. 1.32 cells per original gemma cell) in gemmae grown in 5μmolm^{-2}s^{-1} and similarly (from ca. 0.22 to ca. 1.01) in gemmae grown in 30μmolm^{-2}s^{-1} between 28 and 70 days (see Fig. 3).

Rhizoid production.

After 14 days in culture, some gemmae grown in all levels of PAR from 5 to 90μmolm^{-2}s^{-1} had begun to produce rhizoids. By 42 days of culture gemmae, grown in 5 and 30μmolm^{-2}s^{-1} had generated a significantly greater number than gemmae grown in higher PAR levels ($P<0.05$). The mean numbers of rhizoids increased from ca. 0.18 to ca. 0.57 rhizoids per original gemma cell of gemmae grown in 5μmolm^{-2}s^{-1}, and from ca. 0.17 to ca. 0.67 rhizoids per original gemma cell of gemmae grown in 30μmolm^{-2}s^{-1}. Gemmae grown in PAR of 60 and 90μmolm^{-2}s^{-1} produced significantly fewer rhizoids, only ca. 0.09, and ca. 0.05 rhizoids per original gemma cell after 42 days respectively ($P<0.05$). There was no increase in the number of rhizoids produced by gemmae cultured in either PAR of 60 or 90μmolm^{-2}s^{-1} during culture between 42 and 70 days. There were no statistically significant differences between the mean numbers of rhizoids per original gemma cell of gemmae grown in 5 and 30μmolm^{-2}s^{-1} at any point in the experiment ($P<0.05$ or 60 and 90μmolm^{-2}s^{-1}).

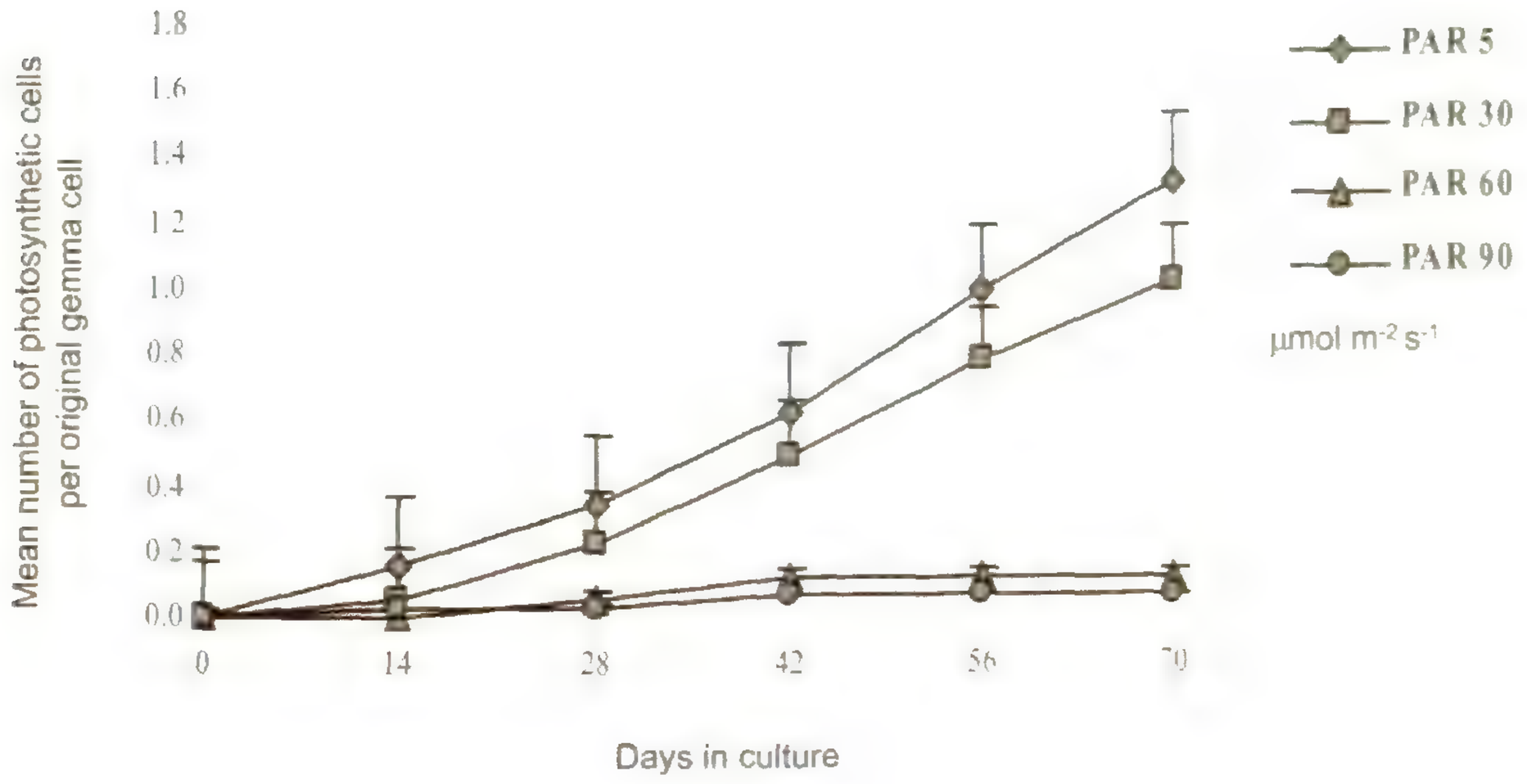

Figure 3. Mean number of photosynthetic cells per original gemma cell (± standard error) of *T. speciosum* gemmae cultured at 20°C in 4 different PAR levels (5-90μmolm^{-2}s^{-1}) against time in culture.

Table 1: The mean number of photosynthetic cells per original gemma cell of *T. speciosum* gemmae cultured in 4 different PAR levels (5-30μmolm^{-2}s^{-1}) for 120 days. The letters signify numbers which are significantly different from numbers with other letters as tested by one-way ANOVA with LSD test ($P<0.05$), n = 120.

PAR (μmolm^{-2}s^{-1})	Days in culture							
	0	14	28	42	56	70	90	120
5	0	0.11	0.45	0.97	1.88	2.64	4.79a	10.40a
10	0	0.15	0.39	0.74	1.25	2.03	3.50b	8.02b
20	0	0.13	0.50	1.04	1.75	2.41	3.89ab	8.12b
30	0	0.11	0.41	0.81	1.45	1.93	2.94b	5.32c

Light experiment II.

Up to 70 days the results mirrored those obtained at the lower light level used in experiment I. After 120 days in culture, most gemmae grown in all levels of PAR tested had produced richly branched filaments in many planes, and rhizoids. Gemmae grown in 5μmolm^{-2}s^{-1} generated the most photosynthetic cells, but all had similar numbers of rhizoids.

Photosynthetic cell production.

After 120 days in culture, gemmae grown in 5μmolm^{-2}s^{-1} had generated significantly greater numbers of photosynthetic cells per original gemma cell (ca. 10.40 cells per original gemma cell) than the others ($P<0.05$) (see Table 1). There was no significant

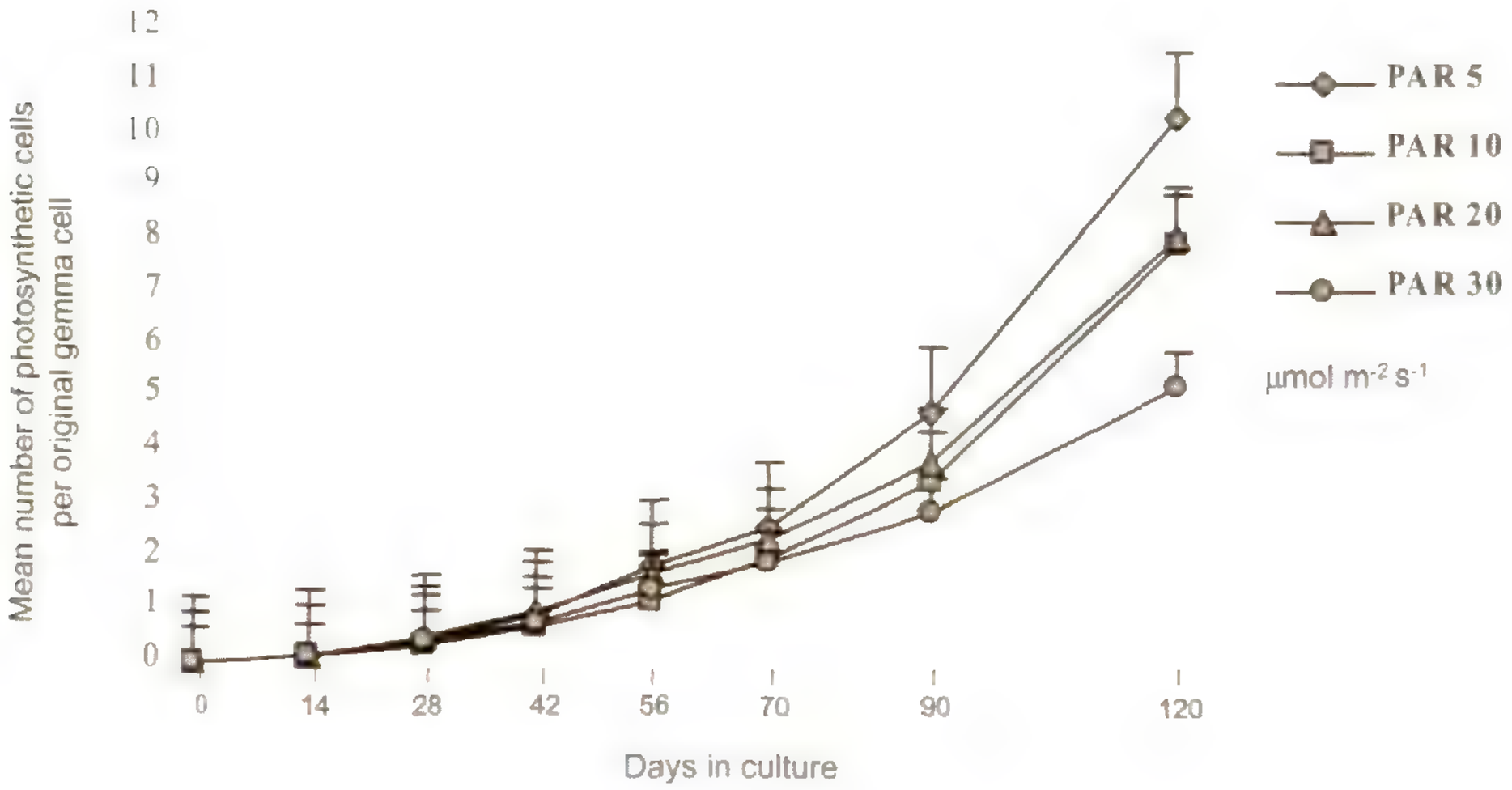

Figure 4. Mean number of photosynthetic cells per original gemma cell (+ standard error) of *T. speciosum* gemmae cultured at 20°C in 4 different PAR levels (5-30μmolm^{-2}s^{-1}) against time in culture.

difference in mean numbers of photosynthetic cells per original gemma cell between gemmae grown in 10 and 20μmolm^{-2}s^{-1} (ca. 8.02 and ca. 8.12 cells per original gemma cell, respectively). Significantly lower mean numbers of photosynthetic cells per original gemma cell (ca. 5.32 cells per original gemma cell) were found in gemmae cultured in 30μmolm^{-2}s^{-1} for 120 days ($P<0.05$) (see Table 1 & Fig. 4).

Rhizoid production.

The mean rate of rhizoid production remained similar in gemmae grown in all levels of PAR during the experiment (ca. 0.01-0.02 rhizoids per original gemma cell per day) (see fig 5). There were no statistically significant differences between the mean numbers of rhizoids per original gemma cell of gemmae grown in all levels of PAR tested by the end of the experiment ($P<0.05$).

Temperature experiment I.

The initial stages of growth of gemmae grown at all temperatures tested were similar. Most gemmae produced photosynthetic cells initially but some of them produced rhizoids first. Most gemmae grown at all temperatures tested produced both photosynthetic cells and rhizoids; more photosynthetic cells were produced than rhizoids in all gemmae that grew.

Photosynthetic cell production.

Significantly fewer photosynthetic cells were produced by gemmae cultured at 28°C than those cultured at 20°C and 24°C, even at 28 days ($P<0.05$) (see Table 2). The mean numbers of cells per original gemma cell were: 20°C, ca. 0.67; 24°C, ca. 0.81; 28°C, ca. 0.24. The mean numbers of photosynthetic cells per original gemma cell increased slightly in gemmae grown at 20°C and 24°C (from ca. 1.36 to ca. 4.35 and from ca. 1.70 to ca. 5.94 cells, respectively) between 42 and 70 days. Between 70 and 120 days in culture, the numbers increased dramatically in gemmae grown at 20°C and 24°C (from

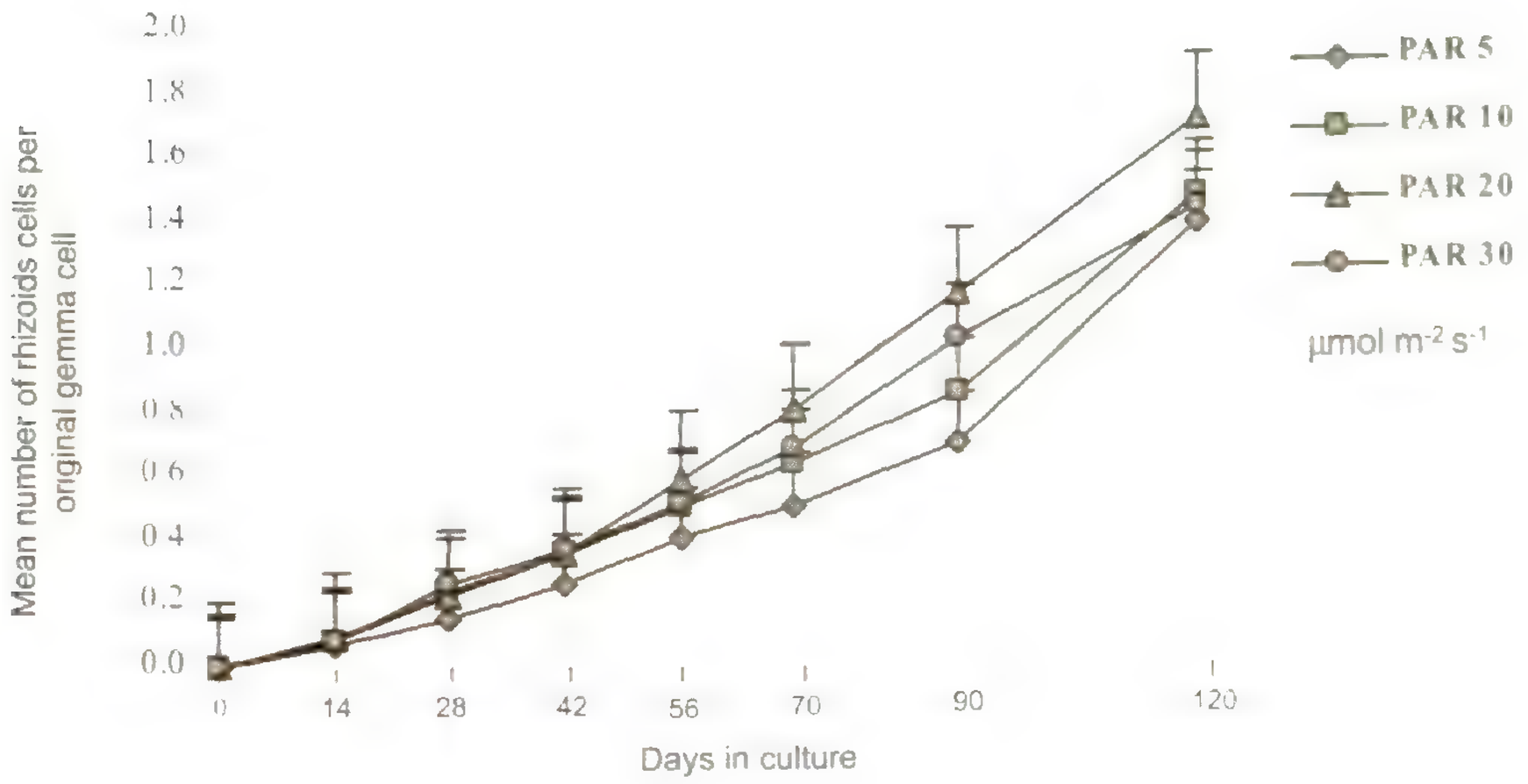

Figure 5. Mean number of photosynthetic cells per original gemma cell (± standard error) of *T. speciosum* gemmae cultured at 20°C in 4 different PAR levels (5-30μmolm^{-2}s^{-1}) against time in culture.

Table 2: The mean number of photosynthetic cells per original gemma cell of *T. speciosum* gemmae cultured at three different temperatures (20, 24, 28C) in PAR of 5μmolm^{-2}s^{-1} for 120 days. The letters signify numbers which are significantly different from numbers with other letters as tested by one-way ANOVA with LSD test ($P<0.05$), n = 90.

Temp (°C)	Days in culture							
	0	14	28	42	56	70	90	120
20	0	0.17a	0.67a	1.36a	2.32a	4.35a	7.69a	15.23a
24	0	0.13ab	0.81a	1.70b	3.01b	5.94b	11.36b	17.96b
28	0	0.07b	0.24b	0.38c	0.46c	0.57c	0.71c	0.78c

ca. 4.35 to ca. 15.23 and from ca. 5.94 to ca. 17.96 cells per original gemma cell, respectively). The numbers increased only slightly (from ca. 0.38 to ca. 0.78) in gemmae cultured at 28°C from 42–120 days (see Table 2 and Fig. 6).

Rhizoid production.

Even by 28 days gemmae grown at 24°C had generated a significantly greater number of rhizoids (ca. 0.29 rhizoids per original gemma cell) than gemmae grown at 20°C and 28°C (ca. 0.17 and ca. 0.04 respectively) ($P<0.05$). Between 42 and 120 days in culture, rhizoid numbers increased dramatically in gemmae grown at 20°C and 24°C (from ca. 0.29 to ca. 1.77 and from ca. 0.50 to ca. 2.17 per original gemma cell, respectively). The mean numbers of rhizoid cells per gemma cell increased only slightly (from ca. 0.11 to

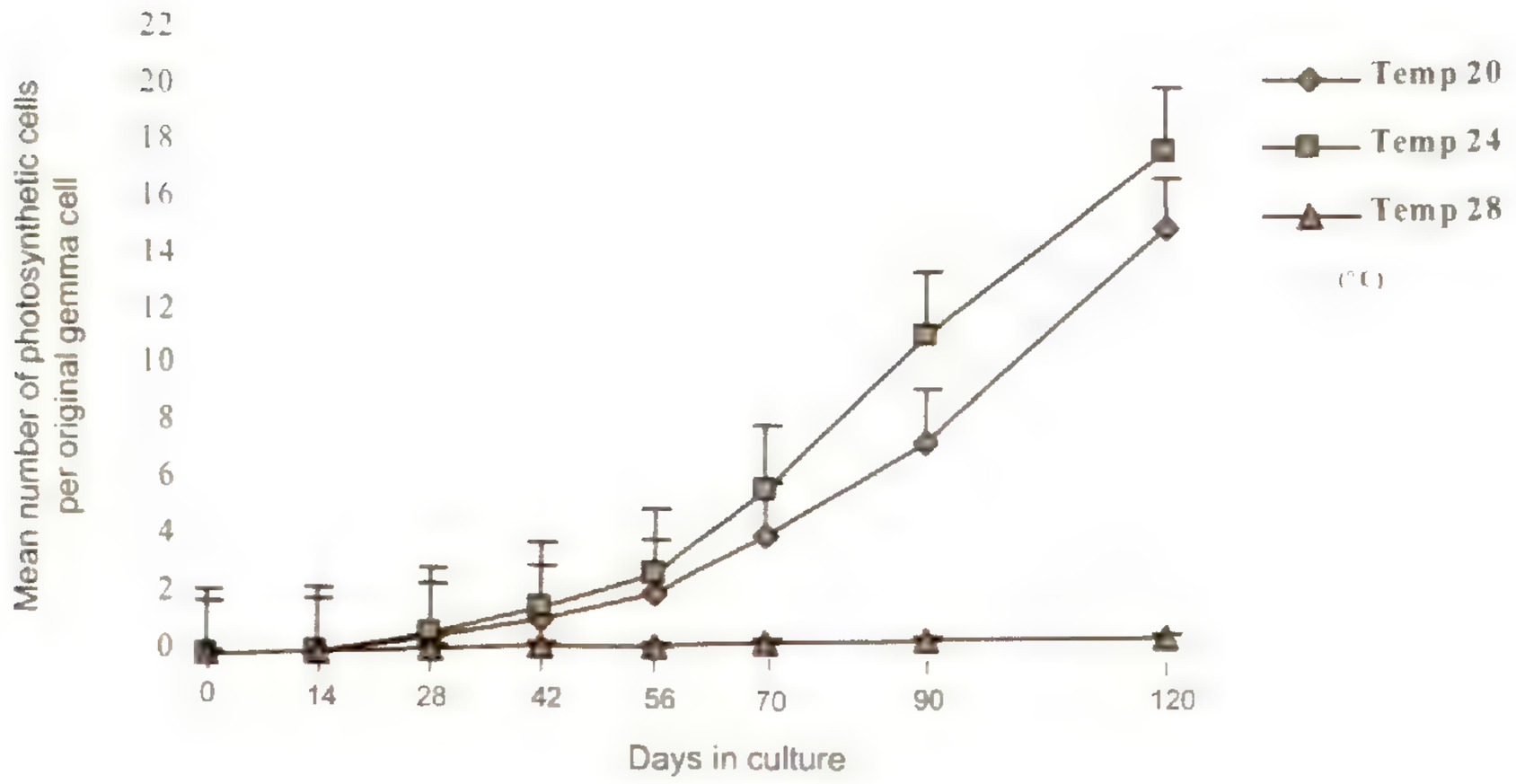

Figure 6. Mean number of photosynthetic cells per original gemma cell (+ standard error) of *T. speciosum* gemmae cultured at three different temperatures (20°C, 24°C, 28°C) in PAR of 5μmolm^{-2}s^{-1}) against time in culture.

ca. 0.51) in gemmae grown at 28°C. After 120 days, the mean numbers of rhizoids per original gemma cell of gemmae cultured at all temperatures tested were significantly different ($P<0.05$). Gemmae grown at 24°C had generated the most, those grown 20°C were next, and those at 28°C had produced the fewest.

Temperature experiment II and comparative analysis.
(For full data see Makgomol, 2001.) After 120 days in culture: fewer photosynthetic cells were produced in 30 than 5μmol$m^{-2}s^{-1}$, for all temperatures tested but the differences were not statistically significant for 28°C; slightly more rhizoids were produced in the higher PAR cultures grown at 20°C and 24°C, similar numbers at 28°C but there were no statistically significant differences in any of the rhizoid data (see Figs 7 & 8).

DISCUSSION

Gemma 'germination'.
The slow start to growth and the variable position of cells in which division begins mirrors spore germination in Hymenophyllaceae. Gemma germination has not previously been described for *T. speciosum*, but has been reported in *T. holopterum* by Farrar and Wagner (1968). The production of photosynthetic cells before rhizoids mirrors spore germination of many species of *Hymenophyllum* and *Trichomanes* (Stokey, 1940). As in spore germination of *Trichomanes*, there is no regular sequence of events in gametophyte growth from gemmae such as is found in typical fern gametophytes of cordate form after spore germination (see also Holloway, 1930; Stokey 1940). Gemmae of *T. speciosum* produce branched filaments which generate both horizontal and erect branches with some rhizoids by around two months in the most favourable conditions supplied in this study, and more filament cells than rhizoids are always produced.

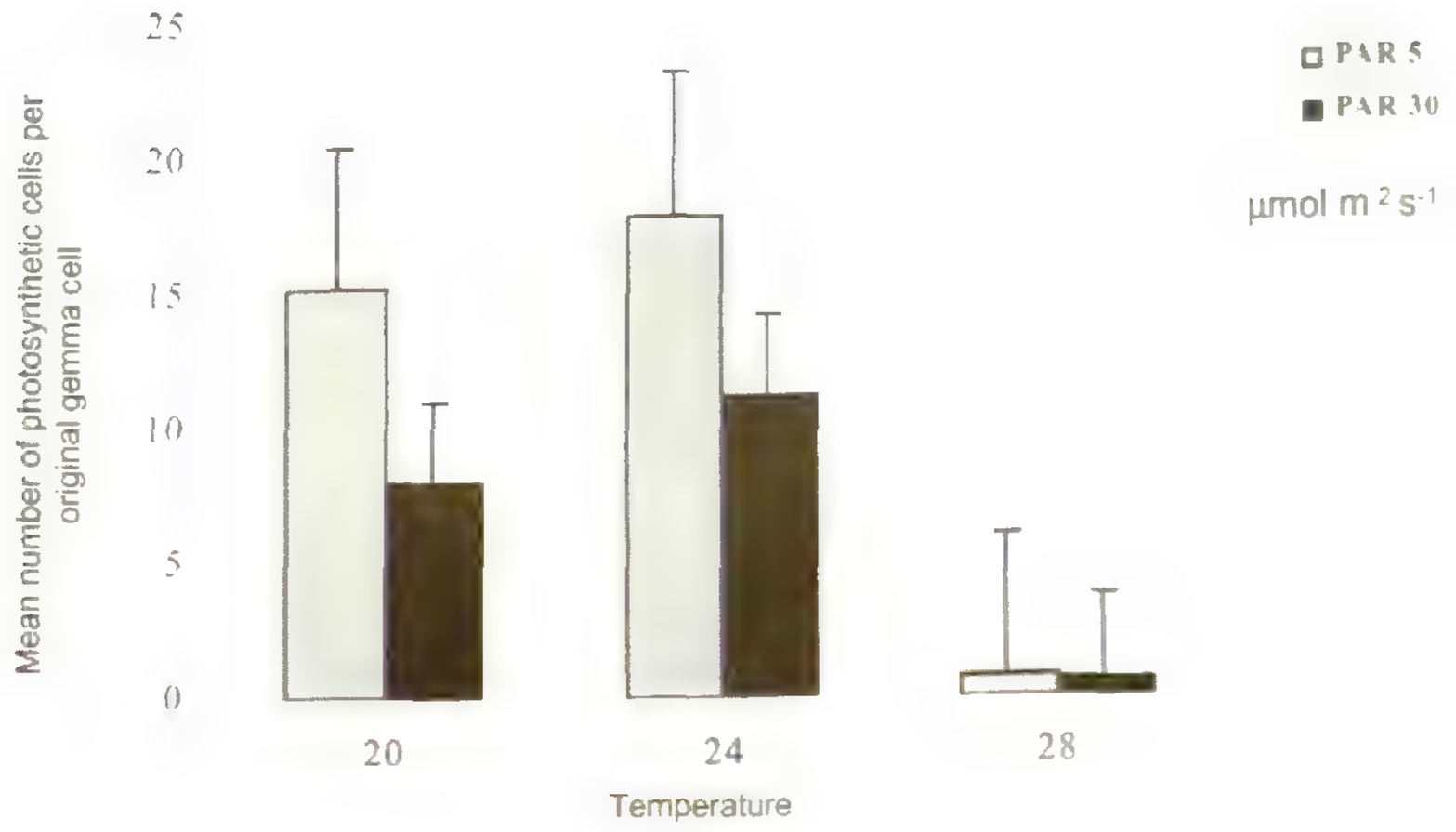

Figure 7. Mean number of photosynthetic cells per original gemma cell (+ standard error) of *T. speciosum* gemmae cultured at three different temperatures (20°C, 24°C, 28°C) in PAR of 5 and 30μmol$m^{-2}s^{-1}$ for 120 days.

As noted by Yoroi (1972) and observed during this study, *T. speciosum* gametophytes grow extremely slowly. They take around eight months to produce further gemmae from gemmae cultured, even in the high temperature, light and aseptic conditions used here. We speculate that *T. speciosum* gametophytes must be incredibly slow growing in British field sites, as gametophytes occur in habitats subject to far lower mean levels of PAR and maximum temperatures than used in our study.

Although some rhizoids were short during the initial stages of cultivation on agar, many became as long as those of field-collected specimens. This means that the rhizoid system of *T. speciosum* is long-lived and extensive, which differs markedly from that of the only other *Trichomanes* gametophyte that has been studied in detail, *T. holopterum*. Rhizoids of *T. holopterum* (Farrar and Wagner, 1968) appear to be too short to function in anchorage or absorption in the manner usually attributed to rhizoids. The finding that those of *T. speciosum* are not geotropic is in line with life in the species' natural habitats, which include floors, walls and frequently roofs of caves. Rhizoid functions of *T. speciosum* are assumed to include absorption and anchoring the gametophytes.

Light experiments.

In the conditions employed herein, levels of PAR in excess of 60µmolm^{-2} s^{-1} damaged photosynthetic cells of gametophytes. Gemmae grown in PAR of 5µmolm^{-2}s^{-1} generated the most photosynthetic cells but gemmae in all levels of PAR up to 30µmolm^{-2}s^{-1} were able to grow. After 120 days in culture, the number of photosynthetic cells generated by gemmae grown in 30µmolm^{-2}s^{-1} was, however, ca. half the number of photosynthetic cells produced by gemmae grown in 5µmolm^{-2}s^{-1}. This finding is in line with the results of Johnson *et al.* (2000), who found no evidence of acclimation of *T. speciosum*, collected in Britain, to different light and temperature conditions. Measurements of gas exchange and chlorophyll fluorescence show that such plants have optimal photosynthesis in PAR levels around 5 to 10µmolm^{-2}s^{-1}, the highest light to which the gametophyte is normally exposed in its natural environment in Britain. This study

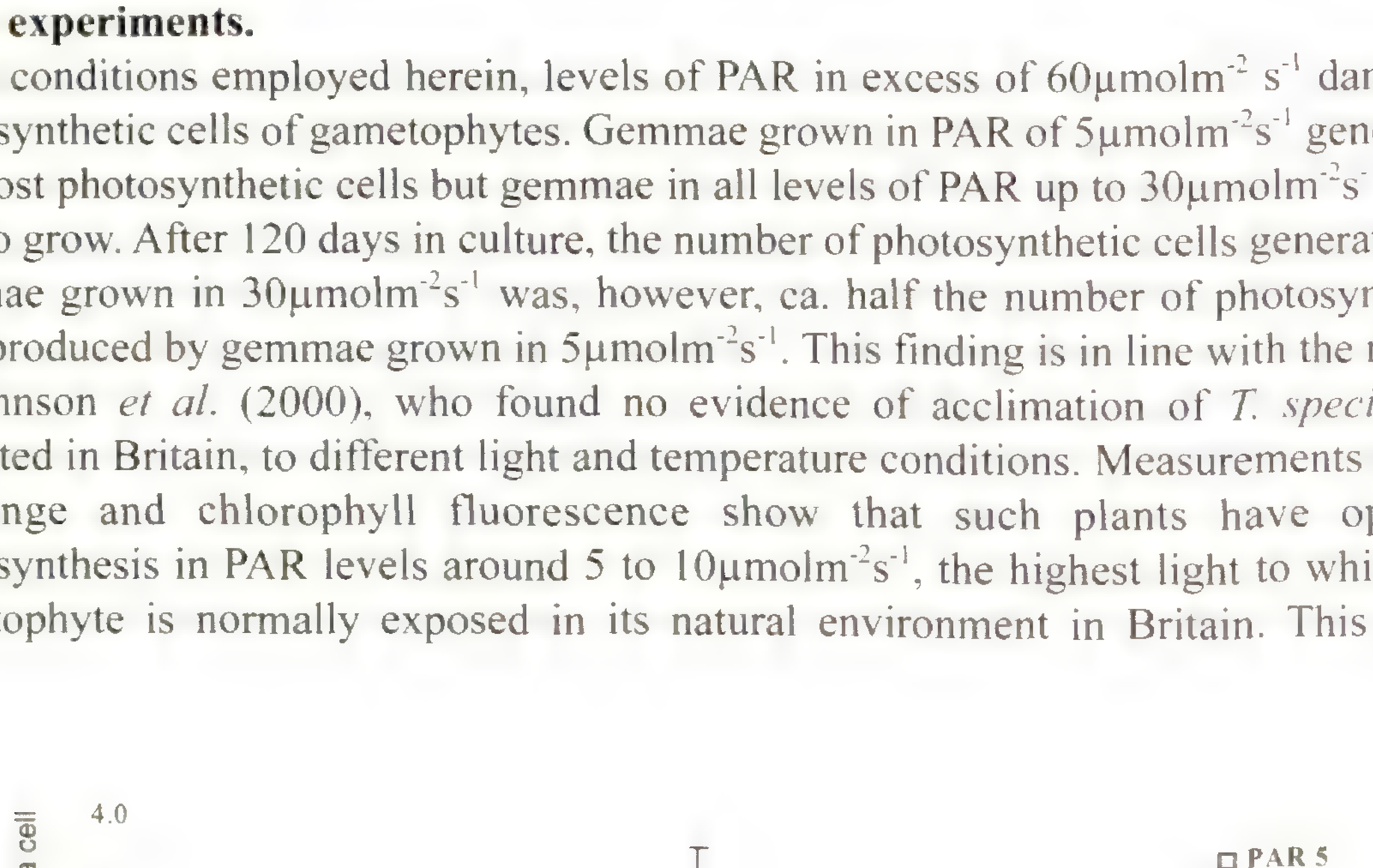

Figure 8. Mean number of rhizoids per original gemma cell (+ standard error) of *T. speciosum* gemmae cultured at three different temperatures (20°C, 24°C, 28°C) in PAR of 5 and 30µmolm^{-2}s^{-1} for 120 days.

supports the contention that the optimal PAR levels for gametophyte growth of British specimens may be around 5μmolm^{-2}s^{-1}.

Temperature experiments.

It is well established that temperature affects both the pattern and the rate of gametophyte development in ferns (Dyer, 1979). *T. speciosum* gemmae grown at a temperature higher than that used in any previous experiments viz 24°C, in PAR of both 5 and 30μmolm^{-2}s^{-1} generated a greater number of photosynthetic cells and rhizoids than those grown at either 20°C or 28°C. Optimal temperatures for *T. speciosum* gametophyte growth may therefore be around 24°C, although this is currently of no direct ecological relevance in British field sites. It does have relevance, however, with regard to the interaction between temperature and light on gametophyte growth. Gemmae grown at 24°C in PAR of 5μmolm^{-2}s^{-1} generated more photosynthetic cells than those grown in PAR of 30μmolm^{-2}s^{-1}. The same was observed at 20°C, which indicates that even at what must be lower rates of respiration, the plants are not able to make use of the extra PAR. In 30μmolm^{-2}s^{-1} PAR rhizoids appeared to be slightly more numerous than in 5μmolm^{-2}s^{-1} but as the differences were not statistically significant it would be unwise to speculate on the possible reasons for this. Different environmental conditions are well known to influence root:shoot ratios in plants and further experimentation on this aspect of the *T. speciosum* response to temperature seems warranted.

Trichomanes speciosum is largely restricted to sunless, sheltered aspects of British sites but with increasing altitude becomes reliant on sunny aspects, thus the altitudinal and geographical distribution suggest that the species is thermophilous (Ratcliffe *et al*., 1993; Rumsey, 1994). Accordingly, the distribution of *T. speciosum* in the British Isles within Europe as a whole suggests a relationship with both humidity and temperature. Although this species is also found in the Azores in sites where the recorded PAR levels are higher than the British field sites, only permanently moist places are colonised. Recording in British field sites during the year 1992-1993 gave a relative humidity above 90% for the majority of the year (see Rumsey, 1994), a condition necessarily replicated in the culture dishes used in our experiments. Thus, the prime determinant for this species' survival may be continual high humidity (see Ratcliffe *et al*., 1993; Rumsey, 1994), with temperature and light having significant and inter-dependent influences.

CONCLUSIONS

This study has provided a vastly more successful suite of conditions for growing gametophytes of *T. speciosum* than any previous work. Constant high humidity, 5μmolm^{-2}s^{-1} PAR and 24°C are suggested for optimum gametophyte growth from gemmae cultured in the media used herein, and could provide the means to raise prolific growth of this rare species. The light compensation point for both the gametophytes and sporophytes of *T. speciosum* was stated to be ca. 2 to 5μmolm^{-2}s^{-1} at 20°C by Johnson *et al*. (2000), and experimental evidence in our study confirmed that British specimens cannot acclimate to higher light levels, even at higher temperatures. Disturbance of habitats (such as tree removal) in habitats could cause a potentially disastrous increase in light (and decrease in humidity).

On the other hand, the establishment of a temperature optimum far higher than ambient temperatures in Britain has implications related to the effects of increasing

amounts of carbon dioxide in the earth's atmosphere. Mean global temperature is increasing as a result of increased concentrations of carbon dioxide from fossil fuel burning, deforestation, and other human activities. Climate changes are likely to vary dramatically from country to country (eg Goldemberg *et al.*, 1995), but it seems likely that Britain will become warmer and wetter in the near future. There will be direct effects of increasing carbon dioxide concentrations on plant growth (Cannell, 1990). Marrs (1990) suggested that vegetation change would involve either the colonisation by new species typical of warmer climates, or the extinction of species typical of colder climates. Bringing together field observations, laboratory-based findings, and distribution data, we can speculate about probable changes to *T. speciosum* in Britain and Europe. The increased periods of drought that are predicted to accompany future global warming in some models would suppress gametophyte colonies and sporophytes could well become extinct (in view of their lower tolerance of environmental extremes than gametophytes, and their rarity). If, on the other hand, increased temperatures are accompanied by higher precipitation in Britain, as predicted by most models, the future for this species looks bright.

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FUNGISTATIC ACTIVITY OF INTERNAL SECRETING HAIRS OF *DRYOPTERIS* RHIZOMES

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A light microscope analysis undertaken in rhizome storage parenchyma of *Dryopteris carthusiana*, *D. dilatata* and *D. filix mas* revealed the presence of numerous secreting hairs in intercellular spaces. Simultaneously, the spaces were occupied by hyphae of several species of saprophytic or pathogenic soil borne fungi i.e. *Acremonium strictum*, *Cylindrocarpon destructans*, *Fusarium sambuccinum*, *Mycellium radicis atrovirens*, *Phialophora cyclaminis*, *Sesquicillium candelabrum* and others. The mycoflora lived endophytically inside the ferns rhizome without any harmful effect. After trials performed on PDA agar in Petri dishes 17 fungal species were isolated and identified. To visualize fungal hyphae in parenchyma the lipofilic fluorochrome [$DiOC_6(3)$] was applied at concentrations 0.1-15 $\mu g\ ml^{-1}$. For determining the living hyphae distribution epifluorescence optics and blue excitation filter (450-490 ηm) were used. (Additionally, chosen phyllopodia were evaluated for presence of fungi along their length.)

Thick layers of lipofilic secretion which covered the heads of secreting hairs, were extracted from parenchyma using diethyl ether (SIGMA) as a solvent and Dragendorf separator. Secretion of glandular hairs contains 20-34 mg of filicin in 100g of fresh mass of parenchyma. Extract from *Dryopteris carthusiana* demonstrated the strongest fungistatic activity against four species of tested fungi (*Acremonium strictum*, *Cylindrocarpon destructans*, *Fusarium sambuccinum* and *Phialophora cyclaminis*) counted according to Abbott formula : $\%H = K_0\text{-}F / K_0 \cdot 100\%$. Reduction of growth rate of fungal mycelia varied from 60.66 to 89.5 % on PDA agar containing 20% of filicin v/v.

Is this phenomenon an example of mutualism?

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PTERIDOPHYTE DIVERSITY ALONG A GRADIENT OF DISTURBANCE WITHIN AND NEAR ABANDONED OPENCAST MINES IN THONG PHA PHUM DISTRICT, KANCHANABURI PROVINCE, THAILAND.

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An assessment of the diversity of pteridophytes in Thong Pha Phum District, Kanchanaburi Province was conducted along a gradient of disturbance within mines, from July 2002 to March 2003. Twelve plots of 5 x 20 meters have been established in three study sites, abandoned opencast mine rocky detritus, remnants of the forest in the mine area and natural forests. Species richness, species diversity and species evenness indices were estimated using Menhinick's, Shannon-Weiner's and evenness indices, respectively. Species similarity was investigated using Jaccard's coefficient. Other physical environmental parameters related to pteridophyte diversity were examined, including light intensity and leaf temperature. Our findings are that species richness and species diversity at these abandoned mines were lower than those for remnants of the forest in the mine area and natural forests, while species evenness was the highest of all. Low Jaccard's coefficient was observed, indicating the difference of pteridophyte species between each sites. Light intensity and leaf temperature showed negative significant correlation with Menhinick's index, but was positively significantly correlated with evenness index. However, significant correlation between those physical factors and Shannon-Weiner's index was not found. From the 36 sampling plots 184 specimens of pteridophytes were collected and identified to 65 species, 1 subspecies, 5 varieties, in 40 genera, from 20 families. It was found that *Cheilanthes tenuifolia* (Burm. f.) Sw., *Sphenomeris chinensis* (L.) Maxon var. *divaricata* (H. Christ) K.U. Kramer and *Lycopodiella cernua* (L.) Pic. Serm. were found only in abandoned mines and tend to be indicator species for disturbed areas. Two terrestrial ferns, namely *Lindsaea ensifolia* Sw. and *Pteris biaurita* L. were commonly found in all study sites. They can be found on rather dry slopes or sandy ground, usually in open areas, but rarely on rocks.

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THE FERN GAZETTE

VOLUME 17 PART 3 2005

CONTENTS

MAIN ARTICLES

Floristics in the 21st Century: balancing user-needs and phylogenetic information
A.R. Smith 105-137

Noteworthy fern discoveries in the Philippines at the turn of the 21st Century
J. F. Barcelona 139-146

Molecular phylogenetic study on Davalliaceae
C. Tsutsumi & M. Kato 147-162

Development of gametophytes from gemmae of Killarney Fern (*Trichomanes speciosum* Willd., Hymenophyllaceae, Pteridophyta)
K. Makgomol & E. Sheffield 163-177

PROGRAMME & POSTERS 102-104

SHORT PAPERS

The pteridphytic diversity in the cloud montane forests from Salta, NW Argentina
E.R. de la Sota & O.G. Martínez 138

Fungistatic activity of internal secreting hairs of *Dryopteris* rhizomes
E.K. Zenkteler & H. Kwaÿna 178

Pteridophyte diversity along a gradient of disturbance within and near abandoned opencast mines in Thong Pha Phum District, Kanchanaburi Province, Thailand.
A. Sathapattayanon & T. Boonkerd 179

INSTRUCTIONS FOR AUTHORS 180

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